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Post-thinning Effects on Water Use Efficiency and Transpiration in a Korean Pine Plantation

잣나무 조림지에서 간벌이
물 이용 효율과 증산에 미치는 영향

2018년 2월

서울대학교 대학원
산림과학부 산림환경학 전공
박 주 한

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지도 교수 김 현 석

이 논문을 농학박사 학위논문으로 제출함
2018년 2월

서울대학교 대학원
산림과학부 산림환경학 전공
박 주 한

박주한의 박사 학위논문을 인준함
2018년 2월

위 원 장 박 필 선 (인)

부위원장 김 현 석 (인)

위 원 임 상 준 (인)

위 원 손 요 환 (인)

위 원 임 중 환 (인)

Abstract

Post-thinning Effects on Water Use Efficiency and Transpiration in a Korean Pine Plantation

Juhan Park

Department of Forest Sciences

Seoul National University

Understanding the underlying mechanism of forest management effects on forest ecosystem function is essential in forest management planning. One of main forest management practices, thinning alters microenvironmental conditions in forest stand. This causes changes of forest function like productivity and water use. The forest management effects have been intensively investigated, and understanding on the underlying mechanisms is increasing. However, they show variations among sites and species.

Korean pine (*Pinus koraiensis*) is one of main plantation species in Korea because it provides various ecosystem services like timber and corn production. Most of Korean pine forests are planted and intensively managed, but understandings on the effects of management practices are limited. Thus, this study aimed (1) to quantify the effects of thinning on tree water use, productivity and water use efficiency, and (2) to develop stand transpiration model relating canopy conductance with

stand structural attributes.

For the first objective, thinning was conducted on Mt. Taehwa with two intensities. The tree water use, productivity and resultant water use efficiency were continuously monitored for four years in a 50-year-old Korean pine plantation. The heavy thinning (30% reduction in stand basal area) significantly improved tree water use and productivity, but light thinning (17% reduction in stand basal area) had minor effects. In addition, the tree size-growth relationship was different by thinning intensity.

For the second objective, stand level transpiration estimated by sap flux density measurement from various stand density and sapwood area was used to develop a canopy conductance model. The canopy conductance model included a set of limitation function by environmental conditions. The reference canopy conductance and stomatal sensitivity to vapor pressure deficit showed a significant relationship with stand sapwood area. With inclusion of this relation, the developed model successfully reproduced the changes of stand transpiration with changes of stand sapwood area and climatic conditions.

The findings of this study on the thinning intensity effects and dominant control of stand transpiration by stand sapwood area help to estimate changes of forest ecosystem function by forest management practices in Korean pine plantations, and can be used as guideline for forest management planning.

Keywords: Thinning, Sapwood area, Size-growth relationship, Productivity, Tree and stand water use.

Student Number: 2011-31027

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Chapter 1. Introduction

1.1 Research background

The causal relationship between structure of ecosystems and their functions is the central question in ecological studies. The structure-function interactions exist in every scale of biological reactions. In forests, structure means the tree's physical arrangements in three dimension (Shugart *et al.*, 2010). In other word, forest structure can be expressed as statistical distribution of trees with different size or with different species on the area. This tree size can be quantified as a diameter at breast height (DBH), canopy height, or biomass.

Natural or anthropogenic disturbances cause sudden and dramatic changes in forest structure. For example, one of common forest management practices, thinning, reduces stand density and distribution of tree size, and changes species composition as well. It causes alteration of interactive strength among trees, which lead to changes of ecosystem function like productivity and water use. The effects of forest structural changes on forest function have gained much attention with increasing anthropogenic influence on forest ecosystem. The causal mechanisms underlying in this forest management practices have been intensively investigated, but these forest management effects show large spatial and temporal variations (Forrester and Bauhus, 2016; Bohn and Huth, 2017) and is also scale-dependent. These bring difficulties in precise estimation

of forest management effects on specific species in specific region.

The most important structural feature to be changed by thinning is leaf area index (LAI), because the majority of important terrestrial processes like photosynthesis and transpiration are occurred in leaves. LAI is defined as total one-sided leaf area per unit ground area or half of total intercepting leaf area per unit ground area (Chen and Black, 1992). It can be measured directly by stripping and measuring area of leaves, which is infeasible due to destructive and time and labor consuming characteristics. On the other hands, indirect measurement techniques like LAI by hemispherical photography, light-interception and reflectance are widely used. Because the amount of intercepted light is dependent on leaf area in light pathway, comparison of light incident with and without canopy can be used to estimate LAI (Kocsis *et al.*, 2006). However, the characteristics of light interception are affected by vegetation type, vertical leaf distribution pattern, and leaf angles and color. In addition, it shows high degree of seasonal variations. These difficulties in LAI measurement make the necessities of using more simple structural variables.

Stand sapwood area (SA) can be also suggested as main influencing forest structural feature. Because the role of SA is supplying water to leaves (Shinozaki *et al.*, 1964a, b), SA shows high correlation with stand LAI (Waring *et al.*, 1977). Even though this SA-LAI relationship can be affected by climatic differences, and stand age and density (Berninger and Nikinmaa, 1997), the easiness and simpleness in SA measurement

make SA as an useful forest structure variable. Thus, the changes in forest functions by thinning practices should be interpreted as difference in LAI or SA.

In Korea, forests cover more than 60% of the land and most of forest are reforested and continuously managed. With the increasing importance in forest ecosystem service, the quantification of forest function such as amount of carbon sequestration and water yield gains more interests. However, the studies on Korean forest have focused mainly on structural characteristics. For example, many studies have reported structural characteristics on Gwangneung forest (Lim *et al.*, 2003), pine forest in human-dominated landscape (Kamada and Nakagoshi, 1993), Baekdudaegan mountain range (Cho *et al.*, 2004), structural development after fire disturbance (Lee *et al.*, 2004b), *Quercus mongolica* forest (Suh and Lee, 1998), and *Picea jezoensis* forest (Jang and Park, 2010). On the other hands, some studies have focused on forest functional characteristic alone, reporting seasonality of forest productivity on broadleaved and coniferous forest (Kwon *et al.*, 2009b), changes of productivity by monsoon (Kwon *et al.*, 2009a), evapotranspiration in complex terrain (Kang *et al.*, 2009), and fine root production and turnover rate (Son and Hwang, 2003).

The large proportion of forest, especially plantation areas are under continuous management. The changes of forest productivity and water use by forest management practices gain much attention due to important role of forest in mitigating climate change effects. However, a little

studies link forest management practices and changes of forest function in Korea (Hwang and Son, 2006; Kim *et al.*, 2009; Lee *et al.*, 2010b). To generalize the forest management effects, the interactions in forest management practices and forest function should be quantitatively evaluated. The models considering these evaluated interactions can be used to test the general applicability, and could help to estimate the changes of forest function by forest management induced structural changes.

1.2 Research objectives

This study aims to find the effects of forest thinning on forest function in a Korean pine plantation. More detailed objectives are (1) to identify the effects of thinning on tree water use, productivity and water use efficiency, and (2) to develop stand transpiration model relating canopy conductance with stand structural attributes.

Chapter 2. Literature Review

2.1 Korean pine plantations and management

Korean pine (*Pinus koraiensis*) is a native species in eastern Asia (Korea, northern China, far eastern Russia, and Japan). It occupies moderate altitude in its northern distribution range, but grows on high altitude in its southern range. It is considered as climax species due to shade tolerant characteristics (Shao *et al.*, 1994). It is sensitive to drought, wind stress, and salinity. In natural forest, pure Korean pine stands are rarely existed, and generally coexisted with *Quercus* and *Acer* species. It grows well on mountain side with well-drained soil, but less on mountain ridge due to dryness and windy environments.

In Korea, natural Korean pine forests are almost disappeared, and remains on some high altitude mountains. However, its high economic and cultural values have made the Korean pine main plantation species. Through the long reforestation history, it is widely distributed throughout South Korea, and occupying about 4% of total forested area (KFS, 2017). It provides important economic services such as timber and corn production. Due to the its vulnerability to changing climatic conditions and high economic value, Korean pine forests are intensively managed. At the beginning of Korean pine plantation, tree seedlings are planted with 3000 trees ha⁻¹, and the weeds are controlled by mowing. At the sapling stage, thinning is conducted at 5 to 10 years after planting to

remove competitive tree species and suppressed trees. At adult stage, pruning and thinning are generally applied. Thinning types can be classified into 4 categories. Low thinning leaves tallest trees in the stand by removing the low crown trees. Crown thinning removes middle or upper canopy trees to make favorable environmental conditions for the best dominant and codominant trees. Selection thinning searches and selects the qualified trees to release lower trees. The systematic thinning is conducted to control the stand density by removing trees depending on predetermined patterns like spatial arrangements without considering of crown class (Graham *et al.*, 1999). The thinning intensity is decided appropriate stand density regarding to the target mean diameter. For example, to produce large-diameter (diameter at breast height: 45 cm) log, stand density is controlled to 250 trees ha⁻¹ through 3-times thinning treatments. The first thinning treatment is conducted at 25 years after planting with leaving 800 trees ha⁻¹, and the second thinning treatment is conducted at 10 years after first thinning with removing half of trees. The third thinning treatment is conducted at 25 years after second thinning with 250 trees ha⁻¹ target stand density, and the final harvesting is conducted at 90 years after planting (KFRI, 2012). To produce medium-diameter (diameter at breast height: 35 cm) log, stand density is controlled to 400 trees ha⁻¹ through 2-times thinning treatments. The first and second thinning treatments are conducted at same years with former case, and final harvesting is conducted at 70 years after planting. For the small-diameter (diameter at breast height: 24 cm) log, stand density is

controlled to 1000 trees ha⁻¹ through single thinning treatment at 25 years after planting, and final harvesting age is 40 years (KFRI, 2012). However, the management effects are not thoroughly investigated and understandings on Korean pine forest dynamics are limited.

There have been limited number of studies on Korean pine plantations in Korea. For example, biomass and carbon distribution into various forest carbon pools is analyzed in age-sequence Korean pine plantation (Li *et al.*, 2011). Canopy closeness is closely linked to soil moisture availability and is a key factor in seed germination rates of Korean pine (Lee *et al.*, 2004a). Changes of climatic conditions causes reduction of site index of Korean pine plantations with regional variation (Kim *et al.*, 2014). Korean pine forest shows higher fine root biomass with higher nitrogen and less phosphorus concentration than nearby oak forest (Kim, 2012). Heavy thinning causes accumulation of more biomass due to the diameter and crown width growth enhancements and reduced mortality (Choi *et al.*, 2014).

On the other hands, many of studies on Korean pine have been conducted in northern China. For example, natural Korean pine-broad-leaved mixed forest shows bivariate distribution characteristics, not univariate distribution (Li *et al.*, 2012). The biodiversity changes after clearcutting are responded differently by climate change and human disturbances (Chen and Li, 2003, 2004). Corn harvesting by human has negative effects on pine seed production, quality and regeneration, and is also linked with populations of vertebrate species. However,

preventing harvesting activities does not lead to improved regeneration of pine (Piao *et al.*, 2011). Microenvironmental regulations such as controlling canopy opening degree promote growth of diameter and height of Korean pine in secondary forests (Cong *et al.*, 2011). Forest thinning changes the composition and structure of Korean pine forest, which shows thinning-intensity related variations (Wu *et al.*, 2016).

In summary, the dynamics of Korean pine plantations are understood a little, and the forest managements effects on Korean pine plantations are rarely understood. Moreover, any studies are not relating the water use of Korean pine plantation with forest management practices. The studies on forest stand water use are enabled by following sap flux density measurement techniques.

2.2 Transpiration estimation by sap flux density measurement

Xylem sap flux density measurement techniques have been widely used to quantify the tree-level water use. After the suggestion of using heat as a tracer of sap flow with theoretical background (Marshall, 1958), various methods have been successfully developed. These methods can be distinguished into two categories – (1) methods to measure total sap flow in whole xylem section, and (2) methods to measure sap flux density which describe the amount of sap flow through the certain area of xylem.

The first category methods have advantage in whole-tree water use estimation, but have limited to access the sap flow variation within the xylem. Two methods - stem heat balance (SHB) and trunk heat balance (THB) - are generally used to measure sap flow. Stem heat balance method can be applied to herbaceous or small (< 125 mm) woody stems, and trunk heat balance method can be applied to large (> 120 mm) woody stems. However, both methods have based on same principle of heat balance. In SHB method, heat is applied to the entire stem area, and is lost via conduction in vertical and radial direction and convection by sap flow movements. The method measures the amount of heat applied and lost by conduction, and the difference between two measurements is used to calculate the convective heat loss by sap flow. In THB method, heat is applied by the electrodes, and conductive heat loss laterally into neighbor sapwood area is additionally considered (Smith and Allen, 1996). Because they assume that additional heat input or loss does not exist, poor contact between thermocouple and stem could generate huge errors and proper protection by gauge is necessary. This gauge protection could generate physical and physiological damage to stem which could result in stem or branch death (Wiltshire *et al.*, 1995). The sheath thermal conductance which controls the heat loss through protective gauges shows significant seasonal and size-dependent variation. In addition, natural vertical temperature gradients and heat storage variation within stem can produce erroneous estimation of plant water use (Grime and Sinclair, 1999).

The second category methods include continuous heat sap flux density methods and heat-pulse sap flux density methods. In general, continuous heat methods require the empirical calibration to related measured temperature and sap flux density (Granier, 1987; Nadezhdina *et al.*, 2010), but heat-pulse methods are based on fundamental physical equations of heat transfer via conduction and convection (Vandegehuchte and Steppe, 2012a, b). Continuous heat methods include thermal dissipation probe and heat field deformation methods, and heat-pulse methods include compensation heat pulse, T_{max} , heat ratio, calibrate average gradient and Sapflow+ methods. Each of these methods has differences in measurement range, sensitivity to natural temperature gradients, and wound effects corrections (Vandegehuchte and Steppe, 2013). Because any single method is not superior to other methods, selection of sap flux density measurement methods is less important than reducing measurement errors by proper sensor installation due to all of these methods shares similar sources of errors.

All of sap flux density methods use insertion of heater and reference probes into sapwood. Thus inaccurate installation of probes is a main source of measurement errors. When heater and reference sensors are closed located, reference probe has thermal interferences by heater sensor which cause the reduction of temperature differences between two probes. In addition, parallel installation of two probes is critical in accurate measurement of temperature differences (Burgess *et al.*, 2001). Moreover, probe insertion itself could be obstruct to xylem water flow

(Green *et al.*, 2003), and it could also induce the formation of wound tissue around the probes (Moore *et al.*, 2010; Wullschleger *et al.*, 2011). These direct and indirect wound effects lead the underestimation of sap flux density and correction of these effects should be applied.

Among the above methods, thermal dissipation probe (TDP) method is most widely used due to its reliability, simplicity, and economic feasibility. It relates the temperature differences between heater and reference probes and sap flux density, but needs the zero flow conditions for sap flux density calculation (Granier, 1987). However, zero flow conditions are not always appeared due to nocturnal xylem water transport for refilling stem water storage, and water loss under high atmospheric vapor pressure deficit condition (Lu *et al.*, 2004). Thus, detection of real zero flow condition is crucial in sap flux density estimation by TDP methods, and this requires empirical based practices and heuristic approaches.

The empirical relationships between temperature differences and sap flux density in TDP method was originally developed to be applied generally regardless of tree species and location. However, many studies have raised questions on its generality and have reported that species- or even tree-specific calibrations are necessary (Lundblad *et al.*, 2001; Bush *et al.*, 2010; Hultine *et al.*, 2010; Rubilar *et al.*, 2017). Even though much of differences in calibration can be explained by measurement errors such as difference in sensor design and materials, wound effects (Wullschleger *et al.*, 2011), and proportion of non-conductive xylem

(Clearwater *et al.*, 1999; Paudel *et al.*, 2013), still different physiological characteristics among tree species bring specific concerns in using TDP method.

2.3 Stand transpiration estimation by canopy conductance model

Canopy conductance controls the exchange of water and carbon between vegetation and the atmosphere, and plays an important role in terrestrial water and carbon cycles. Because the half of the water input into terrestrial ecosystem by precipitation is lost by plant transpiration (Jackson *et al.*, 2000; Schlesinger and Jasechko, 2014), understanding the regulatory relationships in canopy conductance and environmental factors is important. Since the early finding on stomatal regulation by environmental factors and external electric stimulation (Darwin, 1898), regulatory mechanisms on stomatal conductance have been extensively investigated (Kriedemann *et al.*, 1972; Damour *et al.*, 2010). However, leaf-level measurements are failing to extrapolate to canopy-level response, due to complex heterogeneity within canopy and related light or atmospheric water vapor environmental variability. Thus, studies on canopy conductance model (Jarvis and McNaughton, 1986; Whitehead, 1998; Engineer *et al.*, 2016) have been relied on whole-tree or stand-level water use measurements.

Since 1970s, various methods including lysimeters (Edwards, 1986; Allen *et al.*, 1991), radioactive or stable isotope (Waring and Roberts,

1979; Dawson *et al.*, 2002), energy balance based sap flux measurements (Granier, 1987; Swanson, 1994), and eddy-covariance techniques (McMillen, 1988) have been used to quantify the whole-plant water use. Each of these methods has its own advantages and disadvantages. For example, lysimeters techniques have high measurement sensitivity, but is expensive to install and maintain. Isotope techniques are non-destructive, but rely on mass-balance relations which have uncertainties in estimation of every component (Phillips and Gregg, 2003). Eddy covariance techniques are also non-destructive and measure the evapotranspiration directly, but hard to separate transpiration and evaporation. Energy balance based sap flux techniques are inexpensive and easy to apply, but have uncertainties from empirical calibrations.

Even though the increasing understandings on physiological regulation mechanism on stomatal conductance, majority of canopy stomatal conductance models are based on semi-empirical relations. These semi-empirical models can be classified into two types: (1) phenomenological models, and (2) models partly incorporating the stomatal regulation mechanisms. Phenomenological models are represented by multiplicative model (Jarvis, 1976b). In general, stomatal conductance is affected by five main environmental variables: (1) solar radiation (Q), (2) air temperature (T_a), (3) atmospheric vapor pressure deficit (D), (4) soil water potential, and (5) carbon dioxide concentration. The observed canopy stomatal conductance can be estimated by maximum conductance and its serial limitations by each environmental

constraint. Due to little fluctuation of carbon dioxide in short time scale, other four variables are generally considered in daily or seasonal time scale models. The soil water contents can replace the soil water potential, because it is easy to measure. On the other hands, 'Ball-Berry' model (Ball *et al.*, 1987) describe the canopy stomatal conductance as a function of photosynthesis. This model also mainly requires the empirical relationship between stomatal conductance and photosynthesis, but photosynthesis is generally estimated by mechanistic biogeochemical model (Farquhar *et al.*, 1980). Due to that, it shares some features with mechanistic models.

Even though the many disadvantages in Jarvis type conductance model like necessities of measurement in wide range of environmental conditions, and temporal variations in the empirical relationship, Jarvis type models are still widely used due to their simplicity and easy to incorporating into other models like global circulation models. They also separate the response by each environmental constraint, and easy to parameterize by the boundary line analysis.

Chapter 3. Effects of thinning intensities on tree water use, growth, and resultant water use efficiency of a 50-year-old Korean pine plantation over four years

3.1 Abstract

This study investigated the effects of thinning intensities on tree water use and growth of a 50-year-old Korean pine plantation for four years. Thinning was conducted with two intensities (light thinning, heavy thinning, and control) in March 2012. Tree water use was estimated from sap flux density using Granier-type thermal dissipation sensors on 84 of total 103 trees. Tree diameter growth was measured in 97 trees with a dendrometer and converted to aboveground biomass increment using an allometric equation. Sap flux density increased initially in both thinning groups, but the effects of light thinning decreased over time. In the heavy thinning plot, sap flux density was stimulated for the entire study period. While light-thinning affected little on tree growth, tree diameter growth significantly increased from second year and this enhancement increased with time in the heavy-thinning plot. The tree diameter and growth rate were positively correlated in the light-thinning plot and negatively correlated in the heavy-thinning plot. The enhancement of sap flux density and diameter growth caused higher tree water use and tree level

aboveground net primary productivity in heavy-thinning plot. Due to higher water use in the heavy thinning plot, increase in tree-level water use efficiency was observed in the high growth year only. Our results indicate that physiological responses of trees differed depending on thinning intensity and heavy thinning is an appropriate management practice for mature pine plantations.

3.2 Introduction

Forests affect the local weather conditions by changing the atmospheric composition through photosynthesis and respiration (Bonan, 2008). They also change the land surface albedo and affect energy partitioning into latent and sensible heat fluxes. These roles of forests in regulating regional or global weather are sensitive to changes in the physical and physiological characteristics of forest cover. The characteristics of forest cover are closely related to stand density, stand age, and species composition and are altered by natural disturbances or anthropogenic interference, such as forest management practices. Among various forest management practices, thinning or removal of some trees from the forest is widely conducted to produce more valuable and large-diameter timber. It reduces competition among the remaining trees, lowers the risk of natural fire, and helps to maintain a healthy forest (Kerr and Haufe, 2011).

Structural changes in the forest canopy due to thinning alter the microclimatic conditions within the forest. For example, light

distribution within the forest canopy is largely affected by leaf area index, crown structure, and canopy openness. Thinning increases canopy openness and reduces the fraction of absorbed light within the canopy (Hale, 2003). It also augments soil water availability by reducing the intercepted water loss (Breda *et al.*, 1995; Aussenac, 2000; Ganatsios *et al.*, 2010) and causes the groundwater levels to rise (Jutras *et al.*, 2006). These microclimatic changes could improve growth conditions for the remaining trees and understory species. Thus, thinning enhances growth (Aussenac and Granier, 1988; McDowell *et al.*, 2003; Anning and McCarthy, 2013) and photosynthetic efficiency (Gauthier and Jacobs, 2009) in the remaining trees. However, a short-term decline in the growth of remaining trees, which is called “thinning shock,” has also been widely reported (Harrington and Reukema, 1983; Dore *et al.*, 2012). Owing to the recent increase in drought duration and intensity due to changes in precipitation patterns (Trenberth, 2011), attention should be paid to thinning as a drought mitigation procedure. Thinning enhances drought resistance by reducing water stress due to decrement of interception loss and stand transpiration (Gebhardt *et al.*, 2014). Trees in thinned stands show sustained growth under drought conditions and high resilience to severe drought (Kohler *et al.*, 2010). However, this enhancement under drought conditions reduces with stand age; in fact, older stands that are thinned become more prone to drought (D'Amato *et al.*, 2013). In *Pinus* species, thinning promotes not only basal area increment and water use efficiency, but also increased light interception

and nutrient availability (Warren *et al.*, 2001). Similar to other species, thinning improved drought resistance and recovery in *Pinus* species, but these were short-term effects (Sohn *et al.*, 2016). These positive effects could be offset by high vulnerability to insect damage and mortality which might be caused by trunk or root damage during thinning procedure (Zhang *et al.*, 2016).

In conclusion, thinning effects can differ depending on the site water availability and capacity of tree species to adjust to sudden changes in environmental conditions. In addition, the magnitude of thinning effects depends on but is not always proportional to the degree of thinning intensity. Several studies have reported that light thinning stimulates individual tree growth, while heavy thinning hampers growth (Harrington and Reukema, 1983; Laurent *et al.*, 2003; Jimenez *et al.*, 2011). Other studies have reported that the thinning effects increased positively with thinning intensity (Makinen and Isomaki, 2004b; Zhang *et al.*, 2006). However, the enhancement of growth with increase in thinning intensity appeared only in young stands, and this trend was reversed in old stands (Juodvalkis *et al.*, 2005). In addition, the impact of thinning intensities is affected by site location, and it is more intense at windward sites than at leeward sites (Pérez-de-Lis *et al.*, 2011).

Thus, the objective of the present study was to quantify the effect of thinning intensities on water use and growth of individual trees, which could help providing guidelines for the appropriate thinning intensity in mature Korean pine plantations.

3.3 Material and Methods

3.3.1 Study site

The study was conducted at Mt. Taehwa in central Korea (37.18N, 127.18E, 190 m a.s.l.) (Fig. 3.1). The area is undulating, with a 9–10 m difference in elevation, and two streams, in which water flows only after heavy rainfall events, are located in the northern and southern parts of the experimental plot. The 30-year mean annual temperature at the nearest weather station is $11.4 \pm 0.6^{\circ}\text{C}$, and the mean annual precipitation is $1,355.8 \pm 300.2$ mm. The soil is silty loam and the mother rock is granite mixed with gneiss. The majority of forest is composed of *Quercus* species (58.8%), with Korean pine (*Pinus koraiensis*) occupying 20.1% (165 ha) of the area. Our 0.5 ha study plot was established within a 16 ha portion of a 50-year-old Korean pine plantation.

The stand is composed of single overstory species, Korean pine, and some understory species such as *Toxicodendron trichocarpum* (Miq.) O. Kuntze, *Rhododendron yedoense*, *Magnolia kobus* DC., and *Zanthoxylum schinifolium* Siebold et Zucc. These understory species occupied less than 10% of the total basal area (*BA*) and were not included in the stand transpiration calculation. The Korean pine plantation was planted in 50 years ago, and thinning was conducted for two times

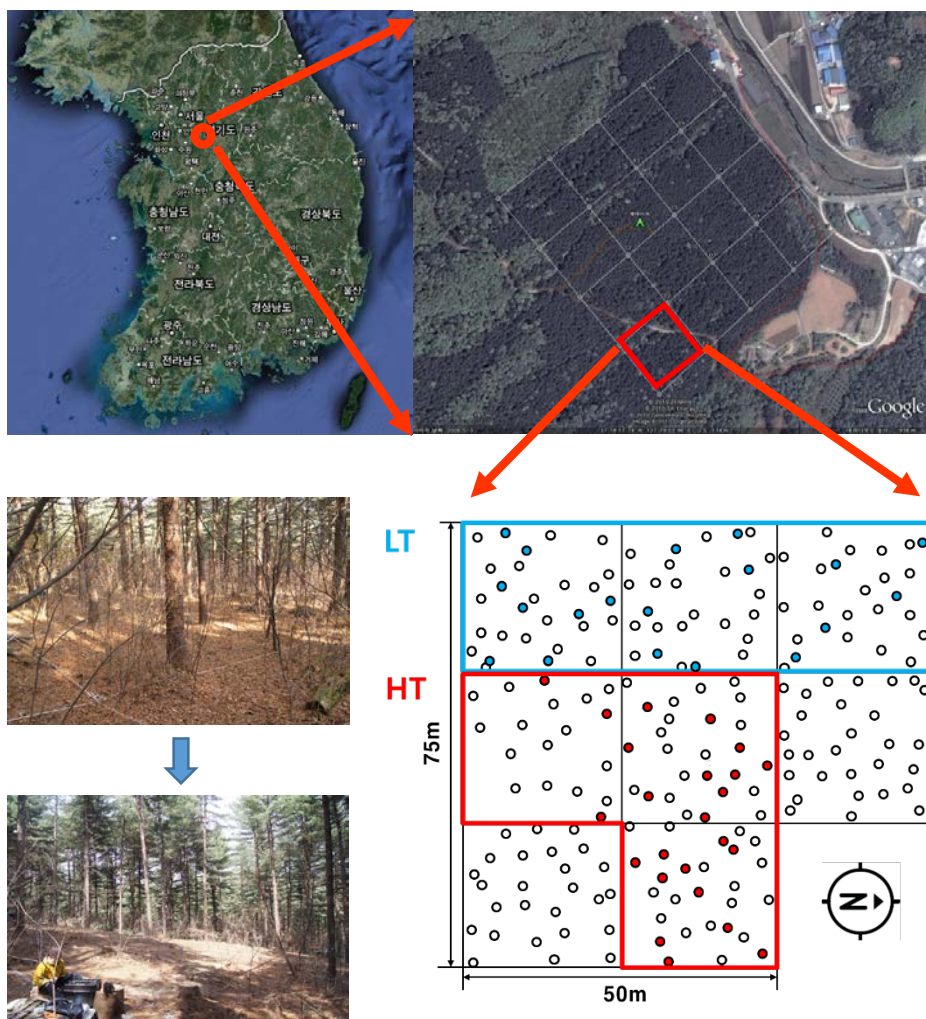


Figure 3.1. (Top) Location and aerial view of the study site (image from google map) and (Bottom right) schematic diagram of thinning. Circles indicates location of trees and colored circles indicate removed trees in light-thinning (LT) and heavy thinning (HT) plot. (Bottom left) Photos of treatment sites before and after thinning.

3.3.2 Experimental design

In 2011, coordinates were assigned to all trees with a diameter at breast height (DBH) > 2 cm throughout the plot, and their diameters were measured. 25 m by 25 m measurement plots were installed and the coordination of each tree was assigned by distance from southwestern corner point of each plot. Because suppressed trees were removed by thinning and tree health status was not surveyed. The coordinates and DBH were used to compute the competition indices (Hegyi, 1974). Thinning was conducted in March 2012. The two thinning intensities were selected on the basis of target stand densities, which were 400, 320, and 240 trees per hectare in the control (0.125 ha), light-thinning (LT, 0.188 ha), and heavy-thinning (HT, 0.188 ha) plots, respectively. The trees in study plots were planted in 1960s, and thinning was conducted for two times. The first thinning was applied in 1988 and the second thinning was applied in 2000, which causes low stand density in control plot. The light and heavy thinning intensities in this study are based on thinning guideline for Korean pine (KFRI, 2012), and describe the relative difference in thinning intensity, not the absolute intensity of thinning. To minimize the interference due to thinning treatments, we maintained a 5 m buffer zone between the treatments. The trees were cut using chainsaws and removed by hand to minimize disturbances such as soil compaction and physical damage to the remaining trees. Trees were selected for thinning based on three criteria: small DBH, short distance to neighboring trees, and previous treatment history (e.g., pruning).

Thinning resulted in an increase in mean DBH of a stand. It removed *ca.* 27 and 37% of the stand density and *ca.* 17 and 30% of the basal area from LT and HT plot, respectively (Table 3.1).

Table 3.1. Stand characteristics of control (Con), light-thinning (LT) and heavy-thinning (HT) plots before and after thinning. Stand density (SD) and basal area (BA) are expressed per hectare, diameter at breast height (DBH) and competition index (CI) are stand arithmetic means \pm 1 standard error (SE). Leaf area index (LAI) is sum of individual tree's leaf area estimated by allometric equation and specific leaf area within each plot.

| | | SD | BA | DBH | LAI | CI |
|-----|--------|---------------------------|------------------------------------|----------------|-----------------------------------|---------------|
| | | (trees ha ⁻¹) | (m ² ha ⁻¹) | (cm) | (m ² m ⁻²) | |
| Con | | 400 | 27.4 | 29.1 \pm 5.1 | 4.15 | 2.0 \pm 0.5 |
| LT | before | 458 | 30.2 | 28.4 \pm 5.8 | 3.76 | 2.0 \pm 0.6 |
| | after | 333 | 25.1 | 30.9 \pm 4.2 | 2.95 | 1.6 \pm 0.5 |
| HT | before | 408 | 28.6 | 29.4 \pm 5.0 | 3.47 | 1.8 \pm 0.6 |
| | after | 258 | 20.0 | 31.2 \pm 3.9 | 2.30 | 1.2 \pm 0.4 |

3.3.3 Data collection

Sap flux density (J_s) was measured by the Granier's type heat-dissipation probe method (Granier, 1987). This method employs an upper heated probe that is supplied constant power (0.2 W) and a lower reference probe. These two probes were installed at breast height vertically, 10 to 15 cm apart to avoid thermal interference. Each probe consisted of a needle 20 mm long with a diameter of 1.6 mm, and the temperature was measured at the middle of the needle by a T-type thermocouple. The temperature difference between the two probes was measured at 30-second intervals, and the average value over 30 min was recorded by a data logger (CR-1000, Campbell Scientific, USA).

The sensors were installed on 22 of 32 trees in control plot, 36 of 40 trees in LT plot, and 26 of 31 trees in HT plot in March 2012. The trees were chosen to avoid edge effects, and the probes were installed on the outer part (0–20 mm) of the sapwood on the north side of each tree. To measure the radial and circumferential variation in J_s , additional probes were installed on the middle (20–40 mm) and inner parts (40–60 mm) of the sapwood of five trees, and at six directions (0, 60, 120, 180, 240, and 300°) on another three trees. The mid- and inner parts of the sapwood area transport 13.7 and 6.9% of the total sap, and sap flow across sapwood area deeper than 60 mm was assumed to be negligible. J_s of the northern side showed little difference with azimuth-averaged J_s (Moon *et al.*, 2015; Moon *et al.*, 2016); therefore, circumferential variation in J_s was not considered. The trees were considered to have the same radial

variations. Tree water use (TWU) was scaled up by multiplying the measured J_s and relevant sapwood area (Eq. 2.1), as follows:

$$\text{TWU (kg d}^{-1}\text{)} = \sum_{i=1}^3 J_{s_i} A_{s_i} \quad \text{<Eq. 3.1>}$$

where J_{s_i} = the daily mean sap flux density of outer ($i = 1$), mid ($i = 2$), or inner ($i = 3$) sapwood ($\text{kg m}^{-2} \text{d}^{-1}$) and A_{s_i} = relevant sapwood area (m^2).

Meteorological data were measured from a 25-m high walk-up tower located 100 m from the treatment plots. Photosynthetic active radiation (Q) was measured by quantum sensor (LI-190, LI-Cor). Air temperature (T_a) and relative humidity (RH) were measured by HMP-45C (Campbell Scientific), and precipitation was measured by rain gauge (03319-00, Cole-Parmer) at the top of the tower. Vapor pressure deficit (D) was calculated from T_a and RH. Data gap due to sensor damage or power failure in meteorological data was filled using data from a 50-m flux tower that is 50 m from the walk-up tower. Volumetric soil water content (θ) of upper 30 cm of soil layer was measured by TDR sensors (CS-616, Campbell Scientific, USA) placed at three positions on each treatment plot in January 2012 and additional 16 sensors installed in May 2014. All the environmental variables were measured at 30 s intervals, and the average values over 30 min of data were stored in a data logger (CR-1000, Campbell Scientific, USA).

Diameter growth was measured with a hand-made dendrometer band

on nearly all the trees on every plot. The recording was manually conducted 7 to 13 times per year. Annual relative growth rate (RGR) of each tree was calculated by following equation:

$$RGR_i = \frac{\text{diameter growth}_i}{DBH_i} \quad \text{<Eq. 3.2>}$$

where, DBH_i = diameter at breast height of tree i.

These diameter growth values were used to calculate the single tree biomass gain by using the allometric equation (Ryu *et al.*, 2014), which showed consistency with other reported allometric equations on same species (Son *et al.*, 2001; Li *et al.*, 2011).

$$\text{Aboveground biomass (kg)} = 0.2849DBH^{2.0553} \quad \text{<Eq. 3.3>}$$

The annual aboveground net primary productivity of each tree ($ANPP_{\text{Tree}}$) was calculated by difference in biomass at the beginning and end of each year. Tree water use efficiency (WUE_{Tree}) is the ratio between annual $ANPP_{\text{Tree}}$ and TWU.

3.3.4 Gap filling

Major data gaps occurred from June 2012 to July 2012 because of a power failure after a typhoon. At other times during the study period, minor gaps occurred due to sensor damage. Data gaps from individual

trees in J_S were filled using the linear relationship with other trees in the same plot. Data from 10 days before and 10 days after the gap were used, and trees that showed the highest correlation with the data-gap tree were selected as reference trees. The average correlation coefficient was 0.98 and the minimum coefficient was 0.91. Major gaps for which no reference sap flux data were available were filled using the linear relationship between J_S and combination of environmental variables like Q , T_a , and D . Similar to gap filling of a single-tree gap, an empirical correlation was induced using data from 10 days before and 10 days after the data gaps. The average correlation coefficient was 0.78 and the minimum coefficient was 0.64. These gap-filled data were not used in the J_S comparison, but only in total tree water use estimation.

3.3.5 Environmental variables

Environmental conditions varied considerably over the 4-year study period. T_a was similar during the study period; however, seasonal trends differed between the first two years (2012, 2013) and last two years (2014, 2015). T_a was higher during summer in the first two years than in the last two years, and it was higher in the winter during the last two years than in the first two years (Fig 3.2a). Annual mean Q followed the annual rainfall frequency pattern and was highest in 2012 and lowest in 2014 (Fig. 3.2b). Notably, the mean growing season D (Mar–Oct) was similar between wet years, but showed a dramatic difference between dry years (Fig. 3.2c). In 2014, it was 14.0% lower than the 4-year-mean D ,

while in 2015, it was 16.0% higher.

The first two years were generally wet and the last two years were dry. The total annual precipitation was 1685.6 mm in 2012, 1366.9 mm in 2013, 791.5 mm in 2014, and 939.4 mm in 2015 (Fig. 3.2d). In addition, the precipitation distribution pattern was different for wet years (2012, 2013). The rainfall frequency was lowest in 2012 and rainfall was mainly due to two events (summer monsoon and typhoon). There was severe soil drying in spring 2012. The rainfall frequency was highest in 2013. The two dry years (2014, 2015) showed similar precipitation patterns with high rainfall frequency during the growing season, but the spring drought lasted longer in 2014 than in 2015.

These conditions resulted in a distinct combination of environmental variables during the measurement years. In general, 2012 was a wet year with a strong spring drought, 2013 was a wet year with low light, 2014 was a dry year with a humid atmospheric condition, and 2015 was a dry year with a dry atmospheric condition (Fig. 3.2a–d).

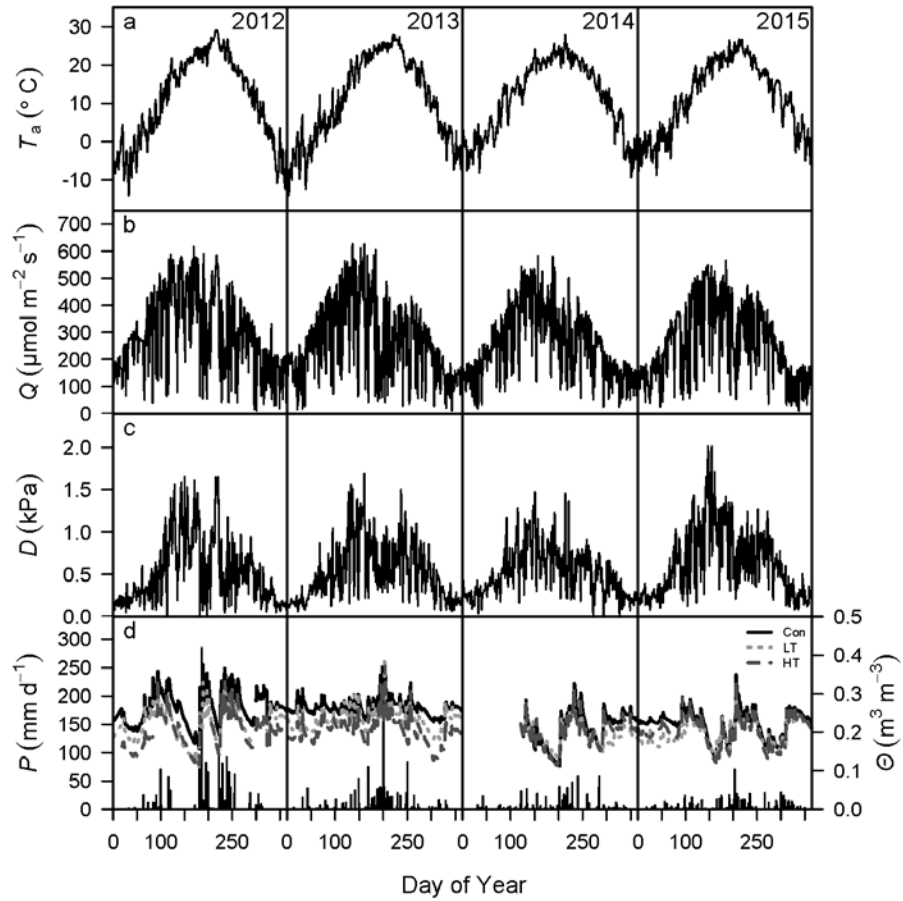


Figure 3.2. Meteorological conditions from 2012 to 2015. (a) Daily mean air temperature (T_a), (b) daily mean photosynthetically active radiation (Q), (c) daily mean vapor pressure deficit (D), and (d) daily mean volumetric soil water content (θ) at 0–30 cm in the control (black), light-thinning (light-grey), and heavy-thinning (dark-grey) plots, along with daily total precipitation (P). The soil water content was measured at three points per plot until April 2014, after which soil water content was measured at six points in the control plot and at nine points in each thinned plot.

3.3.6 Statistical analysis

To evaluate the statistical difference in J_s among plots of different thinning intensities, average daily J_s was used. Diameter growth, RGR, $ANPP_{Tree}$, and WUE_{Tree} of each year were also compared using ANOVA. The normality of J_s and diameter growth data of each plot was assessed by Shapiro-Wilks test. The slope coefficients of linear regression between J_s of control and thinned plots were compared. The sensitivity of environmental variables on J_s and growth was also tested. The difference between thinning treatments during the entire measurement period was statistically evaluated by repeated measures ANOVA with Tukey's LSD post-hoc test. All analyses were conducted in *R* (R Core Team, 2016).

3.4 Results

3.4.1 Effects of thinning intensities on sap flux density and tree water use

The mean J_s of thinned plot significantly increased soon after the thinning practice in March 2012; however, the duration of thinning effects on J_s differed according to thinning intensity (Fig. 3.3). The increment in J_s was continuously enhanced or sustained in the HT plot (+8.0% in 2012, +20.2% in 2013, 40.1% in 2014, and 17.8% in 2015, maximum $p < 0.001$) but weakened with time in the LT plot (+11.1% in 2012, +8.9% in 2013, +9.5% in 2014, and -1.3% in 2015, maximum $p < 0.001$).

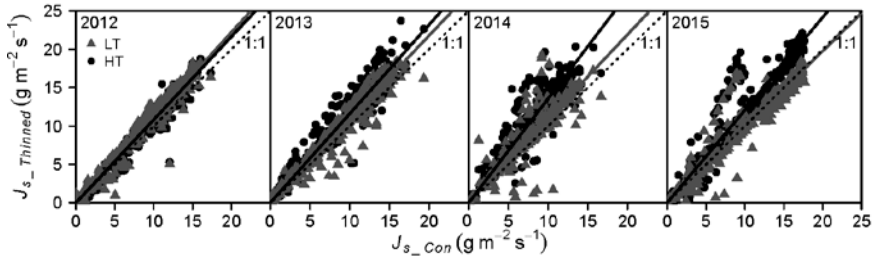


Figure 3.3. Relationship between daily mean sap flux density (J_s) at 0–2 cm of sapwood area in the control plot, light-thinning (LT; grey triangle), and heavy-thinning (HT; black circle) plots from 2012 to 2015. Colored line indicates linear regression line of control and thinned plots, fit with a zero intercept. (LT, $y = 1.111x$, $r^2 = 0.99$, $P < 0.001$ in 2012, $y = 1.089x$, $r^2 = 0.98$, $P < 0.001$ in 2013, $y = 1.095x$, $r^2 = 0.96$, $P < 0.001$ in 2014, $y = 0.987x$, $r^2 = 0.98$, $P < 0.001$ in 2015 and HT, $y = 1.080x$, $r^2 = 0.99$, $P < 0.001$ in 2012, $y = 1.202x$, $r^2 = 0.98$, $P < 0.001$ in 2013, $y = 1.406x$, $r^2 = 0.97$, $P < 0.001$ in 2014, $y = 1.213x$, $r^2 = 0.99$, $P < 0.001$ in 2015).

Although the mean plot J_s increased significantly, TWU was not significantly increased in the first two years owing to large tree-to-tree variations (Fig. 3.4 and Table 3.2). In 2012, mean TWU was 10.8 ± 0.5 , 12.0 ± 0.5 , and 12.1 ± 0.5 kg in control, LT, and HT plots, respectively. TWU in 2013 was similar to that in 2012, but tree-to-tree variations within the same treatment were slightly increased. The mean TWU was 10.6 ± 0.6 , 11.7 ± 0.6 , and 12.4 ± 0.7 kg in the control, LT, and HT plots, respectively. In 2014, when the total precipitation was lowest, trees in the HT plot (16.5 ± 1.6 kg, maximum $p < 0.01$) used more water than those in the control (10.1 ± 1.0 kg) and LT (11.7 ± 0.8 kg) plots. This increase in TWU persisted in 2015 also, and TWU in HT plot (18.6 ± 0.8 kg, maximum $p < 0.05$) was higher than that in the control (15.3 ± 0.8 kg) and LT (14.4 ± 0.7 kg) plots.

The interannual variations in TWU reflected the variations in environmental conditions, but they differed according to thinning intensity. TWU in the control and LT plots showed similar interannual variations, while the HT plot showed a continuous increase in TWU for 4 years. Although precipitation declined by 19% between 2012 and 2013, annual TWU did not reduce in all treatment plots. Despite the huge decrease in annual precipitation, TWU decreased in the control and LT plots in 2014 compared to that in the previous year. In contrast, TWU in the HT plot increased compare to that in the previous year (33.1%). TWU in all plots increased in 2015 compared to that in 2014, reflecting the increase in annual precipitation and atmospheric dryness.

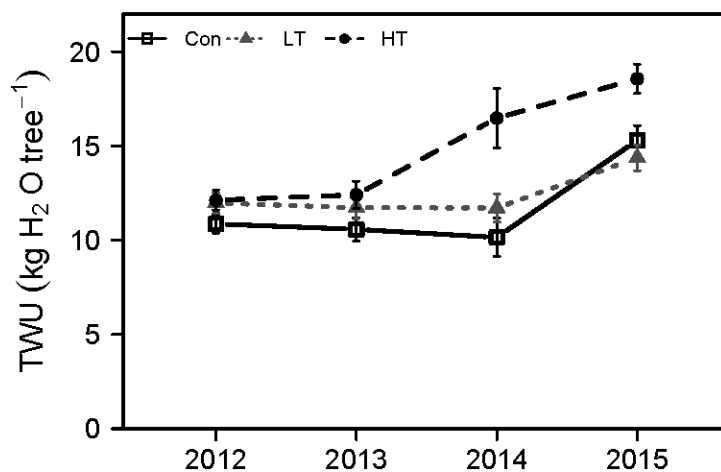


Figure 3.4. Mean daily tree water use of control (Con; open square), light-thinning (LT; closed grey triangle), and heavy-thinning (HT; closed circle) plots from 2012 to 2015. The vertical bars represent the standard error (SE).

Table 3.2. Yearly mean \pm 1 SE of sap flux density (J_s), Tree water use (TWU), diameter growth, Tree level aboveground net primary productivity ($ANPP_{Tree}$), and tree-level water use efficiency (WUE_{Tree}) for control (Con), light-thinning (LT) and heavy-thinning (HT) plots.

| Variable | Year | Con | LT | HT |
|--|-------|------------------------------|------------------------------|------------------------------|
| J_s (g m ⁻² s ⁻¹) | 2012 | 8.4 \pm 0.4 ^a | 9.5 \pm 0.4 ^a | 9.3 \pm 0.4 ^a |
| | 2013 | 8.5 \pm 0.5 ^a | 9.5 \pm 0.5 ^a | 9.9 \pm 0.6 ^a |
| | 2014 | 8.3 \pm 0.8 ^a | 9.6 \pm 0.6 ^a | 13.4 \pm 1.3 ^b |
| | 2015 | 11.4 \pm 0.6 ^a | 10.7 \pm 0.5 ^a | 13.7 \pm 0.6 ^b |
| | Whole | 9.3 \pm 0.4 ^a | 9.9 \pm 0.3 ^a | 11.6 \pm 0.4 ^b |
| TWU (Kg d ⁻¹ Tree ⁻¹) | 2012 | 10.8 \pm 0.5 ^a | 12.0 \pm 0.5 ^a | 12.1 \pm 0.5 ^a |
| | 2013 | 10.6 \pm 0.6 ^a | 11.7 \pm 0.6 ^a | 12.4 \pm 0.7 ^a |
| | 2014 | 10.1 \pm 1.0 ^a | 11.7 \pm 0.8 ^a | 16.5 \pm 1.6 ^b |
| | 2015 | 15.3 \pm 0.8 ^a | 14.4 \pm 0.7 ^a | 18.6 \pm 0.8 ^b |
| | Whole | 11.8 \pm 0.5 ^a | 12.5 \pm 0.4 ^a | 14.9 \pm 0.5 ^b |
| Diameter Growth (mm y ⁻¹) | 2012 | 2.8 \pm 0.2 ^a | 3.2 \pm 0.3 ^a | 3.6 \pm 0.3 ^a |
| | 2013 | 3.6 \pm 0.3 ^a | 4.1 \pm 0.3 ^a | 5.4 \pm 0.3 ^b |
| | 2014 | 2.9 \pm 0.2 ^a | 3.2 \pm 0.2 ^a | 4.3 \pm 0.2 ^b |
| | 2015 | 3.7 \pm 0.3 ^a | 4.2 \pm 0.3 ^a | 5.9 \pm 0.3 ^b |
| | Whole | 3.2 \pm 0.3 ^a | 3.7 \pm 0.2 ^a | 4.8 \pm 0.3 ^b |
| $ANPP_{Tree}$ (Kg C Tree ⁻¹) | 2012 | 3.0 \pm 0.3 ^a | 3.7 \pm 0.3 ^a | 3.9 \pm 0.4 ^a |
| | 2013 | 3.8 \pm 0.4 ^a | 4.7 \pm 0.4 ^a | 6.0 \pm 0.3 ^b |
| | 2014 | 3.1 \pm 0.3 ^a | 3.7 \pm 0.4 ^a | 4.9 \pm 0.2 ^b |
| | 2015 | 4.0 \pm 0.4 ^a | 4.9 \pm 0.4 ^a | 6.8 \pm 0.3 ^b |
| | Whole | 3.5 \pm 0.4 ^a | 4.3 \pm 0.3 ^a | 5.4 \pm 0.4 ^b |
| WUE_{Tree} (g C Kg H ₂ O ⁻¹) | 2012 | 0.78 \pm 0.08 ^a | 0.85 \pm 0.05 ^a | 0.96 \pm 0.09 ^a |
| | 2013 | 1.06 \pm 0.13 ^a | 1.13 \pm 0.10 ^a | 1.49 \pm 0.14 ^b |

| | | | |
|-------|-------------------|----------------------|-------------------|
| 2014 | 1.03 ± 0.14^a | 1.01 ± 0.12^a | 1.05 ± 0.12^a |
| 2015 | 0.72 ± 0.07^a | 1.04 ± 0.11^{ab} | 1.08 ± 0.08^b |
| Whole | 0.89 ± 0.09^a | 1.00 ± 0.07^a | 1.13 ± 0.09^a |

Different letters next to numbers represent significantly different means ($p < 0.05$, Tukey's LSD post hoc tests). The difference in each year was tested by simple ANOVA, and the difference in whole periods was tested by repeated measure ANOVA.

3.4.2 Effects of thinning intensities on diameter growth

Heavy thinning stimulated individual tree diameter growth and RGR, and this growth enhancement was apparent from the second year after thinning (Fig. 3.5 and Table 3.2). The thinning-induced growth enhancement in the HT plot intensified with time ($+27.3 \pm 65.0\%$ in 2012, $+48.7 \pm 46.3\%$ in 2013, $+51.0 \pm 43.9\%$ in 2014, and $+61.4 \pm 46.5\%$ in 2015). Tree growth in LT plot was not significantly different from that in the control plot for the entire study period ($+15.8 \pm 55.6\%$ in 2012, $+14.3 \pm 54.0\%$ in 2013, $+11.6 \pm 53.8\%$ in 2014, and $+13.5 \pm 50.4\%$ in 2015). In 2012, the seasonal growth pattern differed among the plots. While trees in the control and LT plots showed a similar growth pattern, trees in the HT plot showed delayed growth initiation and rapid catch-up after growth initiation. The differences in growth pattern disappeared in 2013, and the HT plot showed a consistently higher growth rate throughout the growing season.

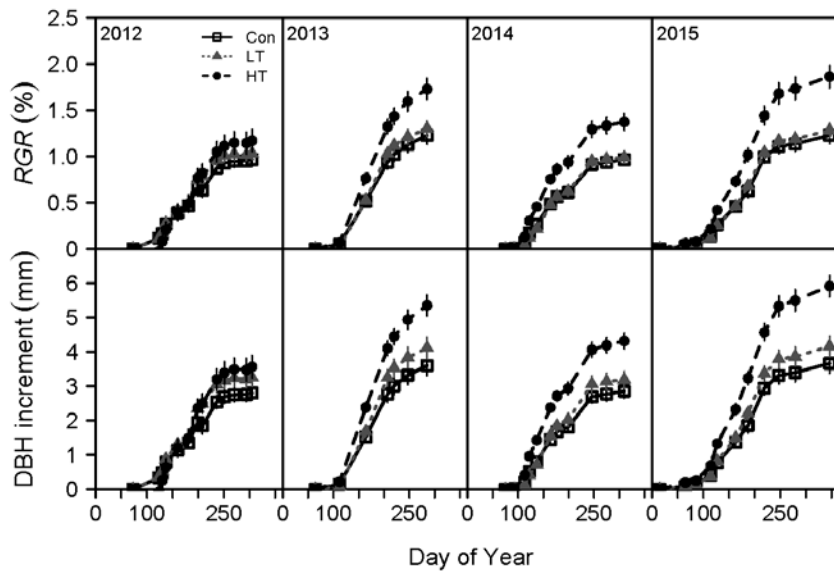


Figure 3.4 Annual patterns of relative growth rate (RGR; top) and absolute diameter growth (bottom) in control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed circle) plots. The vertical bars represent the standard error (SE).

The interannual variations in growth were similar regardless of the difference in thinning intensity; however, the magnitude of variation was highest in the HT plot. This interannual variation in growth was caused by differences in environmental conditions, especially in water availability during the growth onset period. During the years with low annual growth (2012 and 2014), there was severe drought in the spring. In addition, a similar overall growth rate was observed in the control and LT plots despite the huge differences in total annual precipitation and Q . Meanwhile, trees in the HT plot showed a higher growth rate in 2014 than in 2012. There was no spring drought or only a short one during the years with high growth rate (2013 and 2015). As in the low-growth years, trees in the control and LT plot showed similar growth rates in 2013 and 2015 and trees in the HT plot showed higher growth in 2015 than in 2013 (Fig. 3.5).

These growth increment caused the higher $\text{ANPP}_{\text{Tree}}$ in HT plot from the second year after thinning (Fig. 3.6). The trees in LT plot showed consistently statically same but slightly higher $\text{ANPP}_{\text{Tree}}$ than the control plot for the entire study period (minimum $p = 0.247$). The thinning effects in tree growth sustained during the entire study periods, and caused a huge increment in $\text{ANPP}_{\text{Tree}}$ from $3.9 \pm 0.4 \text{ Kg C}$ in 2012 to $6.8 \pm 0.3 \text{ Kg C}$ in 2015.

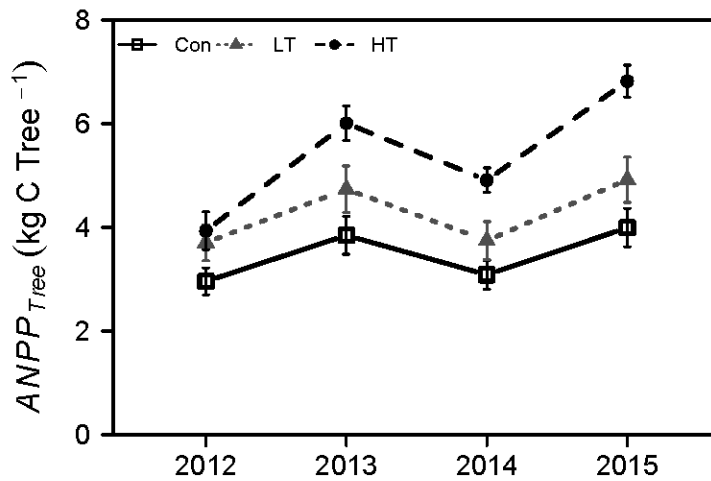


Figure 3.5. Tree-level aboveground net primary production (ANPP_{Tree}) of control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed circle) plots for 4 years. The vertical bars represent the standard error (SE).

In addition, the relationship between DBH and annual growth rate showed a huge difference between the two thinning intensities (Fig. 3.7a). In the LT plot, large trees grew significantly more than small trees, but the opposite trend was seen in the HT plot. These size-growth relationships were observed during the entire 4-year study period. Meanwhile, trees in the control plot showed no significant relationship between tree size and growth rates. Competition intensity, which was estimated by distance and size differences between neighboring trees, was negatively correlated with tree growth rate in the LT plot, whereas there was a significant positive correlation in the HT plot and no significant correlation in the control plot (Fig. 3.7b). In the HT plot, reduction of competition intensity by thinning was positively correlated with tree growth (Fig. 3.7c).

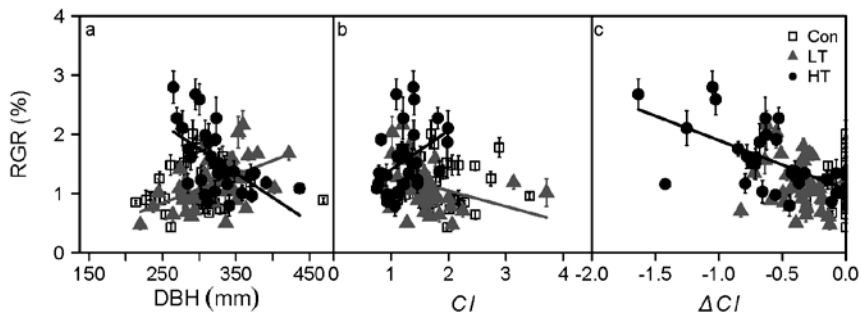


Figure 3.6. Relationship between (a) diameter at breast height (DBH) and 4-year average relative growth rates (RGR), (b) competition index (CI) and RGR, and (c) changes in competition index (ΔCI) and RGR in control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed triangle) plots. Vertical and horizontal bars represent the standard error (SE), and colored lines indicate significant regression between RGR and (a) DBH (LT, $y = 0.005x - 0.362$, $r^2 = 0.25$, $P < 0.001$ and HT, $y = -0.008x + 4.222$, $r^2 = 0.29$, $P = 0.001$), (b) CI (LT, $y = -0.264x + 1.573$, $r^2 = 0.12$, $P = 0.033$ and HT, $y = 0.657x + 0.745$, $r^2 = 0.17$, $P = 0.024$), and (c) ΔCI (HT, $y = -0.8251x + 1.074$, $r^2 = 0.38$, $P < 0.001$)

3.4.3 Effects of thinning intensities on tree water use efficiency (WUE)

Owing to the insignificant effects of LT as well as the synchronized changes in TWU and tree growth in HT, WUE_{Tree} was not affected by thinning (Table 3.2). The only significant difference appeared between control and HT plots in high growth years (2013 and 2015, $p < 0.05$). In 2012, WUE_{Tree} values were 0.78 ± 0.08 , 0.85 ± 0.05 , and 0.96 ± 0.09 g C Kg H_2O^{-1} for the control, LT, and HT plots, respectively. In 2013, the WUE_{Tree} values were 1.06 ± 0.13 , 1.13 ± 0.10 , and 1.49 ± 0.14 g C Kg H_2O^{-1} for the control, LT, and HT plots, respectively. In all plots, WUE_{Tree} was higher than in the previous year (2012), and the HT plot showed a greater increase in WUE_{Tree} than the control and LT plots. In 2014, WUE_{Tree} was reduced in all plots owing to the drought. The WUE_{Tree} values were 1.03 ± 0.14 , 1.01 ± 0.12 , and 1.05 ± 0.12 g C Kg H_2O^{-1} for the control, LT, and HT plots, respectively. In 2015, WUE_{Tree} of the thinned plots recovered with increase in precipitation, whereas it was low in the control plot. The WUE_{Tree} values were 0.72 ± 0.07 , 1.04 ± 0.11 , and 1.08 ± 0.08 g C Kg H_2O^{-1} for the control, LT, and HT plots, respectively. WUE_{Tree} showed different interannual variations after thinning treatment. The control plot showed a decrease in WUE_{Tree} after drought, but WUE_{Tree} recovered in the thinned plots after the drought year. The magnitude of WUE was higher in the HT than in the LT plot (Fig. 3.8).

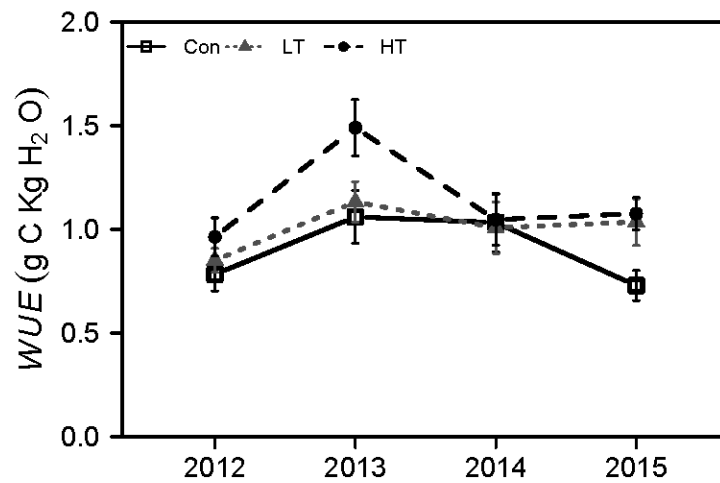


Figure 3.7. Tree water use efficiency (WUE_{Tree}) of control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed circle) plots for 4 years. The vertical bars represent the standard error (SE).

3.5 Discussion

A few studies have quantified the effects of thinning on sap flux density and growth productivity in mature forests (Breda and Granier, 1996; McJannet and Vertessy, 2001); however, studies focused on the effects of thinning intensities are scarce (Makinen and Isomaki, 2004b). In this study, we provide evidence that thinning treatment has considerable effects on water use and growth of trees in mature pine forest and these thinning effects are controlled by thinning intensity.

3.5.1 Effects of thinning intensities on tree water use

After thinning treatment, J_S initially increased in trees at both thinning intensities. The initial increment of J_S is largely due to changes in the light environment, because thinning has little effect on morphological or anatomical adaptations to the changed light environment in such a short period of time (Gebauer *et al.*, 2013). Thinning created more gaps, allowing remaining trees to receive more light, especially on the lower and shaded leaves. This improved light environment induced more leaf-level transpiration as long as soil water was not limited. This initial increase in J_S was not shown in other studies that reported short-term post-thinning stress in transpiration (Reid *et al.*, 2006; Jimenez *et al.*, 2008; Lagergren *et al.*, 2008). Stress induced by thinning might be caused by light stress on previously shaded leaves (Harrington and Reukema, 1983), mechanical damage to shoots or roots during the thinning procedure, or additional freezing damage early in the growing

season due to greater exposure of the canopy to wind. In the present study, the average J_s increase of LT plot in the first year was higher (*ca.* 11.1%) than that of HT plot (*ca.* 8.0%). This finding might indicate that there was higher light stress in the HT plot than in the LT plot.

This initial increment of J_s increased consistently during the four years in the HT plot, whereas enhancement of J_s declined with time in the LT plot and showed no difference with the J_s in the control plot in 2015. The extent of these enhancements depends on thinning type and intensity, site-specific climatic conditions, species and age of remaining trees, and disturbance regime. Especially, it depends primarily on two factors 1) increased water flow through pre-existing sapwood area and 2) increased hydraulic conductivity of newly formed sapwood (Deckmyn *et al.*, 2006). The increased water flow is promoted by the increased water demand of the new conditions such as excess light and soil water, but is constrained by the limited water transport capacity of the existing sapwood. The increased hydraulic conductivity is enabled by the increased tracheid size (Gebauer *et al.*, 2013), formation of new sapwood area (Nadezhdina *et al.*, 2010), or a fertilization effect (Gough *et al.*, 2004).

Although the thinned plots showed increased J_s soon after thinning, high tree-to-tree variation within the plots caused insignificant differences in TWU for the first two years. Owing to both sap flux density increment (Fig. 3.3) and diameter growth increment (Fig. 3.4), TWU increased significantly in HT plot in the third year after thinning (Fig. 3.4). Similar results have been reported in a wide range of tree

species and locations (Medhurst *et al.*, 2002; Gebhardt *et al.*, 2014).

3.5.2 Thinning-induced growth enhancement

In general, water and light are the major limiting factors of tree growth. Water stress is especially notable in the Asian monsoon climate, where most of the annual precipitation occurs during the summer season and there are periodic droughts in the spring and fall. Drought in the spring and fall might disturb phenological development (Borchert *et al.*, 2002), with critical effects on productivity (Richardson *et al.*, 2010). The diameter growth of *Pinus* species in particular is limited by spring drought (Oberhuber *et al.*, 1998; Rigling *et al.*, 2002). Our results showed that reduction of stand density by thinning enhanced the growth of the remaining trees in thinned plot by improving either or both of the limiting conditions (water and light; Fig. 3.5). Thinning promotes photosynthetic capacity by increasing the leaf water potential (Donner and Running, 1986; Gauthier and Jacobs, 2009).

The growth increment of the remaining trees was more pronounced in the HT plot (Fig. 3.5), in accordance with previous results from studies on various tree species (Makinen and Isomaki, 2004a, b; Martin-Benito *et al.*, 2010). The insignificant growth increment in the LT plot might be due to the small removal of the basal area, which was not enough to cause considerable changes (Misson *et al.*, 2005). In addition, the growth rate of trees may increase with tree size, because large trees can support more leaves, which increases the whole-tree photosynthetic rate (Enquist,

2002). However, growth rates are affected not only by tree size but also by competition for light and nutrients as well as environmental conditions. Competition for light is more important for small trees, whereas competition for nutrients affects all trees, regardless of their size (Coomes and Allen, 2007). In addition, sensitivity to competition shows a high correlation with site water availability (Gomez-Aparicio *et al.*, 2011). In the LT plot, thinning did not increase the site water availability because TWU was similar to that in the control plot, and the reduced competition for light did not boost the growth of small trees. Meanwhile, in the HT plot, thinning improved the site water availability as indicated by the huge increment in TWU (Fig. 3.4), which diminished the sensitivity of the trees to competition intensity. Therefore, small trees were benefited the most by thinning and showed higher growth rates than large trees.

3.5.3 Effects of thinning intensities on tree water use efficiency

WUE, which is the ratio of the amount of biomass gain per unit water loss by transpiration, was not increased by thinning treatment except in high growth years (Fig. 3.8 and Table 3.2). As mentioned, thinning reduces competition for water, light, and nutrients. The relative improvement of water and light conditions caused by thinning determines the effects of thinning on WUE. In general, thinning enhances WUE in a light-limited environment (Martin-Benito *et al.*, 2010; Brooks and Mitchell, 2011) rather than in a water-limited

environment (Moreno-Gutierrez *et al.*, 2011; Giuggiola *et al.*, 2015). Thinning increases light interception by individual trees and concentration of nutrients in the foliage, resulting in efficient carbon assimilation. High density stands showed less WUE than the low-density stands especially in shade-intolerant pine forests (Warren *et al.*, 2001).

WUE is controlled more by carbon gain than by water use in mesic areas (Yang *et al.*, 2016). Although there were huge differences in annual precipitation among the study years, soil water status reached the field capacity during summer precipitation in all the years, and soil water content was maintained above 15% during most of the growing periods (Fig. 3.2). Thus, TWU was hardly affected by fluctuation in annual precipitation (Fig. 3.4). In the years with low stand WUE (2012 and 2014), severe spring droughts (Fig. 3.2) hampered tree growth (Huang and Zhang, 2007).

In 2014, a notable combination of environmental conditions was observed: humid atmosphere and drought-affected soil (Fig. 3.2c, d). WUE_{Tree} is controlled by both D and Θ , with D dominating (Yang *et al.*, 2010; Novick *et al.*, 2016). Θ and WUE may have an opposite relationship for low and high D conditions due to failure in stomatal optimization. Under low D conditions, tree water use could be decoupled from Θ owing to loose stomatal regulation. Unregulated stomata resulted in similarly low WUE_{Tree} in all plots. In addition, the leaves that developed during previous humid conditions may fail to adjust their physiological characteristics to dry conditions completely. The huge

reduction of WUE_{Tree} in HT plot was mainly caused by the improved TWU (Fig. 3.4).

WUE_{Tree} increment of thinned plot in 2015 could be explained partly by “memory effects,” which are effects of previous drought on current productivity and water use (Zhang *et al.*, 2014; Yang *et al.*, 2016). Under drought conditions, trees increased their belowground allocation to increase their water uptake capacity. Evergreen conifer trees in particular tend to allocate more biomass to the drought enduring organs (Markesteijn and Poorter, 2009). The combination of improved soil water condition, high D , and previous investment to adapt to drought conditions caused a significant increase in WUE_{Tree} in 2015. Meanwhile, WUE_{Tree} was reduced in the control plot. Although both TWU and $ANPP_{Tree}$ increased over the previous year in the control plot, the increment of water use outweighed that of biomass gain. Owing to higher density in the control plot relative to thinned plot, TWU responded to D more sensitively.

3.6 Summary

Our study shows that thinning enhanced the sap flux density and diameter growth. These positive effects of thinning on tree level water use and growth were more apparent in HT plot than in the LT plot. The interannual variations in water use efficiency indicated that light conditions might be the main driver of positive thinning effects. Other approaches, such as stable isotope analysis in leaves or tree core analysis

could be used to reveal the hidden mechanism of thinning effects.

Our results indicate that thinning by 40% removal of total trees is an appropriate management practice in mature pine forests compared to thinning by 20% removal, and this results in improved tree growth together without loss in water use efficiency.

Chapter 4. Developing Stand Transpiration Model

Relating the Canopy Conductance with Stand

Sapwood Area in a Korean Pine Plantation

4.1 Abstract

Relationship between forest water use and forest structure has been intensively investigated, but underlying mechanism in the spatial and temporal variations of forest water use is not fully explained yet. For improving the understanding on the effects of forest structural changes on forest water use, transpiration from *Pinus koraiensis* stand with various sapwood areas was monitored for 4 years using sap flux density measurements. The stand transpiration used to estimate canopy conductance (G_c) by inverse simplified Penman-Monteith equation, and multiplicative empirical G_c estimation model was developed. The model considered a set of serial limitations of G_c by environmental variables like vapor pressure deficit (D), photosynthetic active radiation (Q), air temperature (T_a) and soil water contents (θ). The relationship between parameters in each limiting function and stand structural characteristics was analyzed. The results showed the dependency of canopy conductance on stand structure. The reference G_c (G_{cref}) and stomatal sensitivity to D (m) had significant relationship with stand sapwood area (SA). Other parameters showed insignificant interaction with SA . Thus,

stand transpiration estimation model which relating the G_c and SA was developed. This model successfully reproduced the changes of stand transpiration with changes of SA and climatic conditions. Since this model uses the simple and easily-measurable structural variable, SA , it can be easily applied to other *Pinus koraiensis* forests, and help to estimate the spatial and temporal variation of stand transpiration.

4.2 Introduction

Forest stand structure such as standing biomass, stand density, species composition has been reported as one of the main controlling factors in forest water use and yield. Many studies have confirmed the effects of forest structure change by natural disturbance or forest management practices on forest water balance (Hornbeck *et al.*, 1993; Sun *et al.*, 2006; Simonin *et al.*, 2007). Significant forest structural attributes in controlling forest water balances have been identified, and spatial variation in an stand sapwood area is one of the most sensitive structural parameter in determining the spatial heterogeneity of forest water use and yield (Vertessy *et al.*, 2001). Sapwood area is highly related with stand leaf area index (Medhurst and L. Beadle, 2002), and is a very useful index due to easiness to measure.

However, estimation of the forest water use by stand sapwood area alone is limited because sapwood area is generally very conservative, which fails to estimation the interannual variations in forest water use. This large temporal variation in stand transpiration is mainly due to

variability in climatic condition, because the radiative energy input to the forest and atmospheric vapor pressure deficit are main drivers of transpiration. The transpiration is controlled by stomatal conductance, which regulate the amount of water loss via stomata to keep the its homeostatic conditions.

These two source of variations can be connected by canopy conductance (G_c), because G_c is mainly controlled by stand leaf area index (or sapwood area) and stomatal conductance. To estimate the G_c , mechanistic and empirical model approaches have been used. Mechanical models consider the response of G_c against plant internal physiological processes like regulation of stomatal guard cell by ion channel and signaling (Wang *et al.*, 2012). On the other hands, empirical models rely on the observed responses of G_c to variations of environmental conditions. They do not give any specific physiological meanings, but have been employed largely at field level analysis due to their simplicity and effectiveness (Mielke *et al.*, 1999; Oren *et al.*, 2001; Blanken and Black, 2004). For example, multiplicative models use a set of limiting functions to modify a maximum conductance accounting the empirical relationships for environmental variables (Jarvis, 1976a).

For developing the empirical models, continuous measurements of G_c under various environmental and structural conditions are essential. Due to the difficulties in direct measurement G_c , indirect measurement of G_c from stand transpiration is widely used (Granier *et al.*, 2000b; Blanken and Black, 2004; Kumagai *et al.*, 2008). Sap flux density measurement

is useful for investigate the stand transpiration at various spatial and temporal scale, due to its wide-range of applicability (Wilson *et al.*, 2001). It can produce continuously reliable measurement of tree-level and stand-level water use at high temporal scale. Especially, this technique is suitable on area with complex terrain structure and various tree species composition such as Korean forest.

Reliable estimation of forest water use is important for forest management planning. To access changes of stand transpiration with structural and environmental variation, stand transpiration model which connect structural attributes and environmental conditions with G_c is developed in this study. The model development processes are compromised with three steps. First, G_c was calculated from stand transpiration estimated by sap flux density measurement. Second, limitation of G_c by each environmental variable was analyzed. Third, limiting function of G_c was related with structural parameters (sapwood area), and tested its applicability with different climatic conditions.

This approach could be more convincing to forest composed with single species having isohydric characteristics. Thus, an even-aged pure Korean pine (*Pinus koraiensis*) forest is selected as target area. Korean pine is one of main planting species in Korea, and providing valuable ecosystem services like carbon sequestration and corn production.

4.3 Material and Methods

4.3.1 Study sites

The study was conducted at Mt. Taehwa in central Korea (37.18N, 127.18E, 190 m a.s.l.) as same as previous study. Detailed explanation on study site can be found in section 3-3-1. The experiments were conducted on 8 sites with different stand density (SD), basal area (*BA*) and sapwood area (*SA*) conditions (Table 4.1). Outer 60 mm of each tree's *BA* is assumed to be conductive *SA*, because sap flow across sapwood area deeper than 60 mm is negligible (Moon *et al.*, 2015). Environmental conditions were measured on 25-m high walk-up tower and 50-m high flux tower. Detailed explanation on environmental measurement can be found in section 3.3.3

Table 4.1. Stand characteristics of experimental plots. Stand density (SD), basal area (*BA*), and sapwood area (*SA*) are expressed per hectare, diameter at breast height (DBH) are stand arithmetic means \pm 1 standard error (SE).

| Plot | SD (trees ha ⁻¹) | <i>BA</i> (m ² ha ⁻¹) | <i>SA</i> (m ² ha ⁻¹) | DBH (cm) |
|------|---------------------------------|---|---|----------------|
| P1 | 400 | 29.2 | 18.2 | 29.9 \pm 1.5 |
| P2 | 375 | 26.1 | 16.8 | 29.5 \pm 1.0 |
| P3 | 300 | 22.2 | 13.9 | 30.4 \pm 1.4 |
| P4 | 325 | 28.1 | 16.8 | 33.0 \pm 1.0 |
| P5 | 300 | 27.7 | 16.0 | 34.1 \pm 1.2 |
| P6 | 400 | 25.6 | 17.0 | 28.3 \pm 1.0 |
| P7 | 250 | 17.6 | 11.4 | 29.8 \pm 0.9 |
| P8 | 225 | 14.7 | 9.8 | 28.8 \pm 0.7 |

4.3.2 Stand transpiration measurement

Stand transpiration was estimated from sap flux density (J_s) measured by the Granier's type thermal dissipation probe method (Granier, 1987). This method employs two probes with upper heating probe and lower reference probe. The temperature differences between two probes is converted to sap flux density by the following equation (Granier, 1987):

$$J_s = 118.99 \times 10^{-6} \left(\frac{\Delta T_{max} - \Delta T}{\Delta T} \right)^{1.231} \quad \text{<Eq. 4.1>}$$

where J_s is sap flux density ($\text{g m}^{-2} \text{s}^{-1}$), ΔT_{max} is maximum temperature difference recorded at zero flux, and ΔT is temperature difference recorded at each time step. Because coefficients in equation 4.1 are highly sensitive to applied heat quantity (Granier, 1987), constant power (0.2 W) is supplied on the heating probe.

Stand level transpiration (E_T) was scaled up by multiplying the measured sapflux density and relevant sapwood area (Eq. 4.2).

$$E_T (\text{mm d}^{-1}) = \sum_{i=1}^3 J_{s_i} A_{s_i} / A_p \quad \text{<Eq. 4.2>}$$

where J_{s_i} is the daily mean sapflux density of outer ($i = 1$), mid ($i = 2$), or inner ($i = 3$) sapwood ($\text{kg m}^{-2} \text{d}^{-1}$), A_{s_i} is relevant sapwood area (m^2), and A_p is the total plot area (m^2). The sapwood area was selected as the

only scaling factor, because total needle mass was highly correlated with DBH (Ryu *et al.*, 2014), which showed high correlation with sapwood area.

4.3.3 Stand transpiration estimation model

The canopy conductance estimated by inversion of simplified Penman-Monteith equation (Jarvis and McNaughton, 1986; Komatsu *et al.*, 2014). This equation assumes equilibrium evaporation is negligible, and can be applied on coniferous plantations which is closely coupled to overhead atmosphere due to their short leaf characteristic length (Whitehead *et al.*, 1984; Kelliher *et al.*, 1993). The equation is expressed E_T as,

$$E_T = \frac{\rho C_P G_c D}{\gamma \lambda} \quad \text{<Eq. 4.3>}$$

where ρ is the density of air, C_P is the specific heat of air, G_c is canopy conductance, D is vapor pressure deficit, γ is the psychrometric constant and λ is the latent heat of water vaporization.

G_c calculated by the relationship between environmental conditions and E_T is used as reference in estimation model. This model uses the sensitivity of G_c against environmental variables, and a set of serial limiting function is applied as following equation (Jarvis, 1976a):

$$G_c = f_1(D) \cdot f_2(Q) \cdot f_3(T_a) \cdot f_4(\theta) \quad \text{<Eq. 4.4>}$$

where $f_1(D)$, $f_2(Q)$, $f_3(T_a)$ and $f_4(\theta)$ are functions expressing the responses of G_c to daily mean vapor pressure deficit (D), photosynthetically active radiation (Q), air temperature (T_a), and soil water contents (θ), respectively. Each response is modeled as following equations:

$$f_1(D) = G_{cref} - m \cdot \ln(D) \quad \text{<Eq. 4.5.>}$$

$$f_2(Q) = \min \left\{ \left(\frac{Q}{600} \right)^\delta, 1 \right\} \quad \text{<Eq. 4.6.>}$$

$$f_3(T_a) = \left\{ \left(\frac{T_a - T_{min}}{T_{opt} - T_{min}} \right) \left(\frac{T_{max} - T_a}{T_{max} - T_{opt}} \right) \right\}^{\left(\frac{T_{opt} - T_{max}}{T_{opt} - T_{min}} \right)} \quad \text{<Eq. 4.7.>}$$

$$f_4(\theta) = \left\{ \begin{array}{ll} 0 & \text{when } \theta < \theta_{min} \\ \frac{\theta - \theta_{min}}{\theta_{max} - \theta_{min}} & \text{when } \theta_{min} < \theta < \theta_{max} \\ 1 & \text{when } \theta > \theta_{max} \end{array} \right\} \quad \text{<Eq. 4.8.>}$$

where G_{cref} is reference value of G_c when $D = 1.0$ kPa, m is slope between G_c and $\ln(D)$, δ is parameter which determine the sensitivity of Q on G_c limitation, T_{min} , T_{max} , and T_{opt} are minimum, maximum and optimum T_a for G_c , respectively, θ_{min} is wilting point where stomata is completely closed by soil water limitation and θ_{max} is soil water content where limitation by soil water does not exist.

All of above parameter values are estimated by gradient-based L-BFGS-B algorithm in the *optim* function in R software (R Core Team, 2016), which minimize the variance between observed G_c and estimated G_c . structural characteristics. Among the parameters, G_{cref} and m are showed large variation between different sites (Oren *et al.*, 1999; Herbst *et al.*, 2008). On the other hands, other parameters like δ show very conservative characteristics regardless of difference in stand structure (Ewers *et al.*, 2008). This indicates that stand structural characteristics can be assumed to have relation with G_{cref} and m , and others not.

To test the compatibility of the stand transpiration model, three different model parameter set-up are compared with the 4-year continuous measurement stand transpiration data from 8 different plots. The first model uses optimized parameter values for each plot and each year (hereafter E1 model). The second model uses G_{cref} and m estimated by relationship with stand sapwood area and optimized parameter values for other parameter in each plot in first measurement year (hereafter E2 model). The third model uses same G_{cref} and m with E2 model, and plot mean values for other parameters (hereafter E3 model).

4.4 Results

4.4.1 Environmental constraints on canopy conductance

Figure 4.1 shows the relationships between environmental variables (D , Q , T_a , and θ) and canopy conductance (G_c). Each plot in Fig. 4.1 represents the limiting interaction by each environmental variable. At first, observe G_c is compared with D . Q is compared with G_c divided $f_1(D)$. T_a is compared with G_c divided $f_1(D)f_2(Q)$. At last, θ is compared with G_c divided by $f_1(D)f_2(Q)f_3(T_a)$. Here, results from P1 in first measurement year are only shown, but same processes are conducted on other plots and other year also.

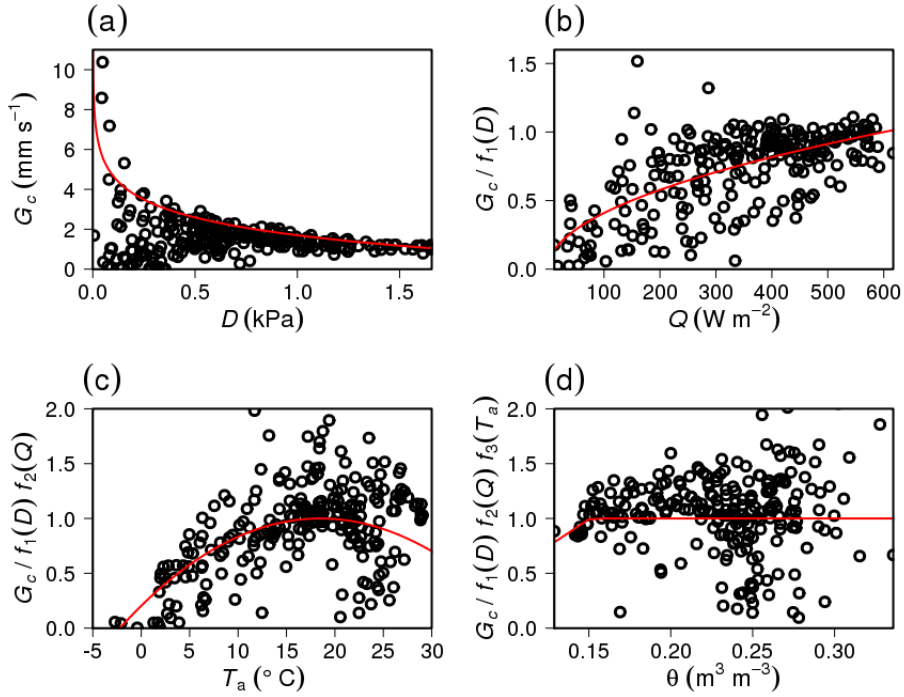


Figure 4.1. Relationships (a) between vapor pressure deficit (D) and canopy conductance (G_c), (b) between photosynthetic active radiation (Q) and G_c divided by estimated G_c by using D only ($f_1(D)$), (c) between air temperature (T_a) and G_c divided by estimated G_c by using D and Q ($f_1(D)f_2(Q)$), and (d) between volumetric soil water content (θ) and G_c divided by estimated G_c by using D , Q , and T_a ($f_1(D)f_2(Q)f_3(T_a)$). The red line in each plot indicates the function expressing the response of G_c to D , Q , T_a , and θ , respectively.

4.4.2 Relationship between parameter values and sapwood area

There are large inter-plot variations in m and G_{cref} . Maximum m (1.37 mm d⁻¹ kPa⁻¹) and G_{cref} (1.74 mm d⁻¹) are about 70% higher than minimum m (0.79 mm d⁻¹ kPa⁻¹) and G_{cref} (1.06 mm d⁻¹). δ shows variation among plots also (maximum $\delta = 0.63$ and minimum $\delta = 0.40$). T_{opt} has less variation among plots than those of G_{cref} , m , and δ (minimum $T_{opt} = 18.5$ °C and maximum $T_{opt} = 21.1$ °C).

The m and G_{cref} showed significant correlation with stand sapwood area (Fig. 4.2(a, b)). The 2nd order regression explains 90.5% of variation in m ($P < 0.001$) and 85.8% of variation in G_{cref} ($P < 0.001$). The regression lines were determined as $m = 0.014SA^2 - 0.362SA + 3.02$, and as $G_{cref} = 0.014SA^2 - 0.334SA + 3.016$, respectively. Other two parameters did not show significant correlation with SA (Fig. 4.2 (c, d)).

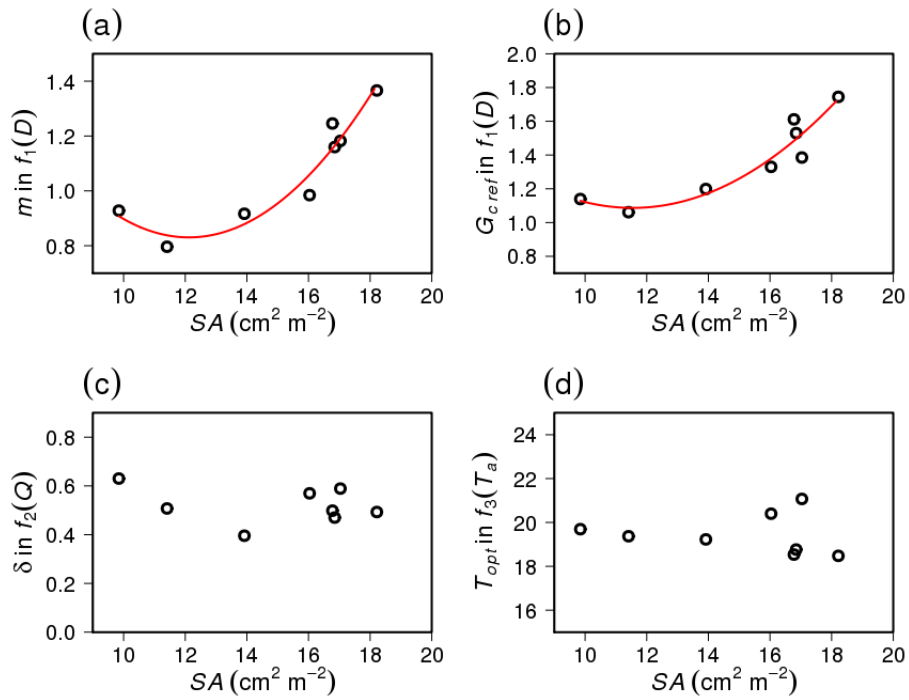


Figure 4.2. Relationship (a) between stand sapwood area (SA) and the slope (m) in $f_1(D)$, (b) between SA and the reference canopy conductance (G_{cref}) in $f_1(D)$, (c) between SA and regression coefficient (δ) in $f_2(Q)$, and (d) between SA and optimum air temperature (T_{opt}) in $f_3(T_a)$. Red lines indicate statistically significant regression between SA and (a) m and (b) G_{cref} , respectively.

4.4.3 Stand transpiration estimated by combination of limiting functions

Fig. 4.3 shows the serial time-steps in estimation of stand transpiration. At first, stand transpiration was calculated by the canopy conductance estimated by using $f_1(D)$ only. This caused the overestimation in spring, monsoon season, and late autumn and winter, when Q is generally low, and resulted in relatively low determination coefficient (adj. $R^2 = 0.624$) (Fig 4.3(a)). When limitation by Q was considered, errors in spring, monsoon, and autumn were reduced, but still showed considerable overestimation in winter time. The determination coefficient was slightly increased (adj. $R^2 = 0.705$) (Fig 4.3(b)). These errors in winter decreased by consideration of limitation by T_a . The estimated E_T reproduced the seasonal variation of observed E_T well, and the determination coefficient was highly increased (adj. $R^2 = 0.805$) (Fig 4.3(c)). The limitation by soil water contents had little effects on stand transpiration estimation, and determination coefficient was not increased (adj. $R^2 = 0.807$) (Fig 4.3(d)).

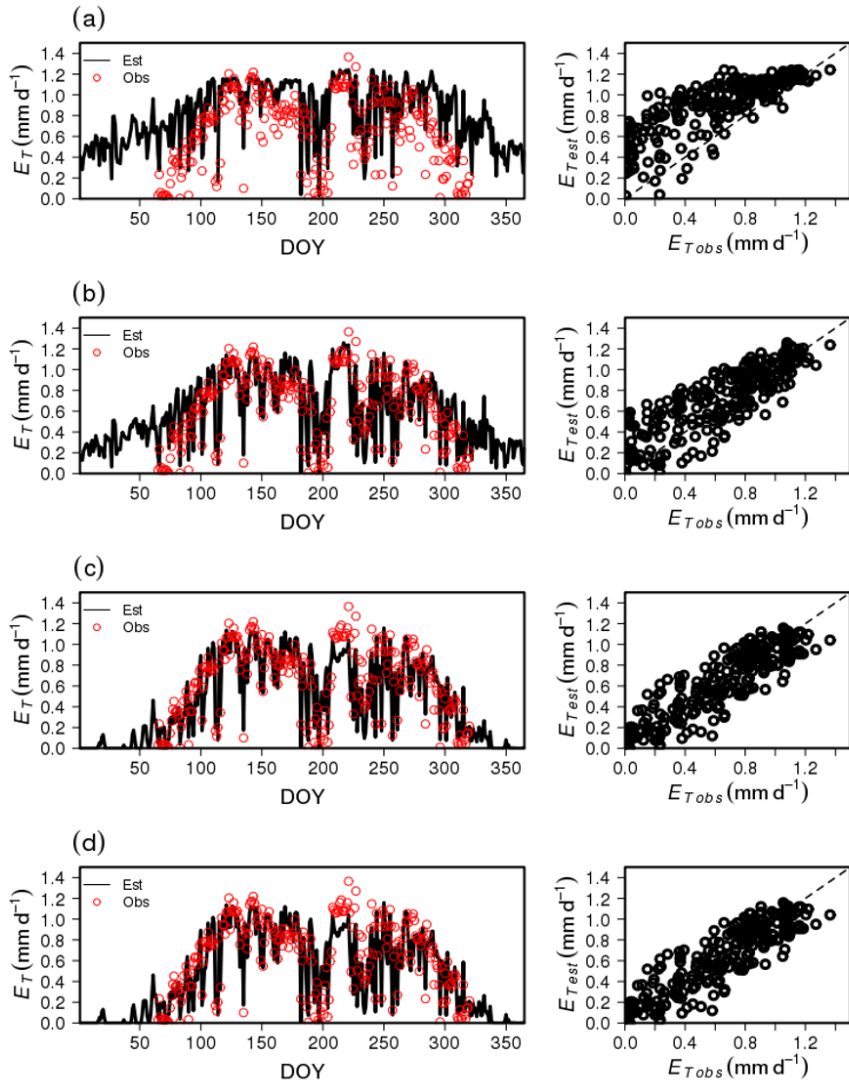


Figure 4.3. Time series of observed daily transpiration (E_T) for P1 in 2012 and ET estimated by stomatal conductance model (a) using D only, (b) using D and Q , (c) using D , Q , and T_a , and (d) using all of variables (D , Q , T_a and θ). The figures in right side show the correlation between estimation E_T and observed E_T .

4.4.4 Model performance evaluation

Fig. 4.4 showed the relationship between observed stand transpiration and estimated transpiration using optimized parameter for each plot and each year (Fig. 4.4(a)), using parameter estimated by relationship with sapwood area and optimized parameter for each plot in 2012 (Fig. 4.4(b)), and using parameter estimated by relationship with sapwood area and average optimized parameter in 2012 (Fig. 4.4(c)). The estimated E_T by the optimized parameters for each year and each plot was strongly correlated with observed E_T ($r = 0.97$, $P < 0.001$). The use of SA related parameters reduced the correlation between estimated E_T and observed E_T ($r = 0.88$, $P < 0.001$). The correlation coefficient showed decrease with year, and showed highest in 2012 ($r = 0.98$, $P < 0.001$), and lowest in 2014 ($r = 0.80$, $P = 0.016$). Other 2 years showed intermediate correlations (in 2013, $r = 0.87$, $P = 0.005$, in 2015, $r = 0.82$, $P = 0.012$). The use of plot mean parameter values slightly decreased the correlation coefficient ($r = 0.86$, $P < 0.001$). Same as previous model, the correlation was highest in 2012 ($r = 0.96$, $P < 0.001$), and lowest in 2014 ($r = 0.73$, $P = 0.039$).

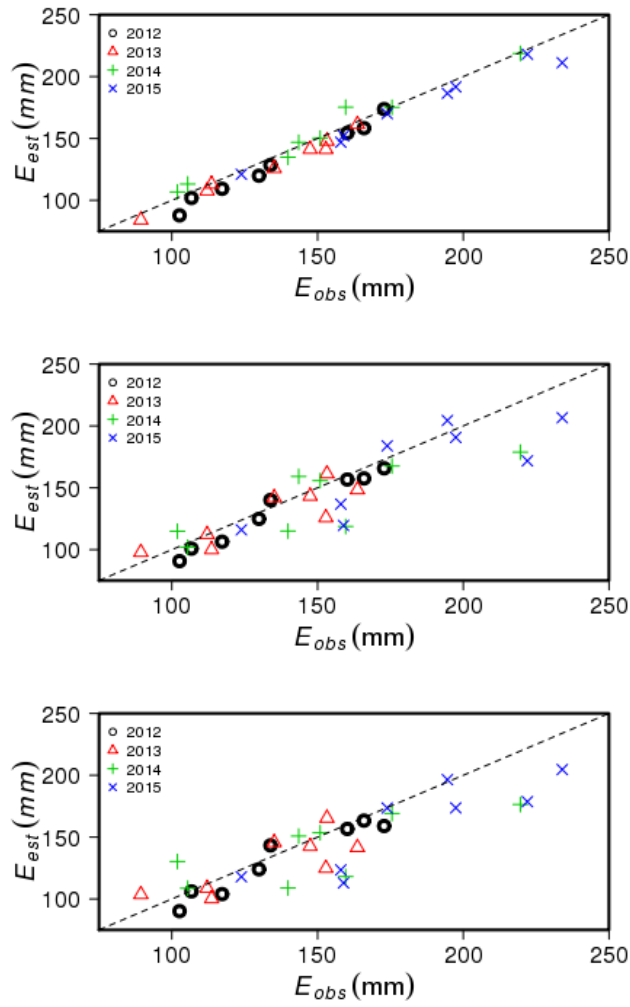


Figure 4.4. Relationship of annual stand transpiration estimated (a) by E1 model, (b) by E2 model, and (c) by E3 model.

4.5 Discussions

4.5.1 Canopy conductance sensitivity to environmental and structural variables

The developed stand transpiration model successfully reproduces the interannual variation in observed E_T at 8 plots with different stand structures for 4 years (Fig. 4.4). It includes the 4 environmental limiting factors such as D , Q , T_a , and θ , and through the serial limitation by environmental variables, model estimated E_T reproduces the seasonal variation of observed E_T (Fig. 4.3). D is most limiting factor in canopy conductance, which explains the 62% of temporal variations of E_T alone. The incorporation of limitation by other environmental variables increases the model performance slightly (Fig. 4.3(b, c)), but θ has no influence in E_T estimation (Fig. 4.4(d)). One reason for this insignificant relation could be that θ is not limiting factor in study forest or at least during the first measurement period when empirical relationship is analyzed. The θ -related reduction in G_c is not observed in other temperate forest (Komatsu *et al.*, 2006), but significant soil water limitation effects have been reported also (Tanaka *et al.*, 2002; Kim *et al.*, 2008).

Limitation by Q increases the model performance in spring, autumn and monsoon season. Asian monsoon region generally experiences dry periods before and after summer monsoon, and this leads decline of hydraulic conductance by embolism associated with D stress (Anderegg *et al.*, 2014). Monsoon reduces the water stress, and tree water use is more affected by available energy. Limitation by T_a has dominant effect on G_c in winter and early spring. G_c shows its optimum under T_a conditions between 15 to 20°C (Gash *et al.*, 1989), and starts to decrease when T_a is below than 15°C (Granier *et al.*, 2000a).

$G_{c_{ref}}$ and m show the significant interactions with stand sapwood area (Fig. 4.2). In general, $G_{c_{ref}}$ has positive relationship with stand leaf area, the ratio of sapwood-to-leaf area and inverse of canopy height (Novick

et al., 2009). However, G_c -SA relationship found on this study is different with previous studies that report saturation of canopy conductance at high LAI (Granier *et al.*, 2000b). This is due to low stand density and sapwood area. The LAI estimated by site-specific allometric equation (Ryu *et al.*, 2014) ranges from 2.3 to 4.15, and is much lower than reported LAI (≈ 6) at saturation of G_c observed.

4.5.2 Interannual variation of parameters

The parameter values in each limiting function are relatively conservative, and shows minor interannual variations (Fig. 4.5). This is partly caused by the physical characteristics of target species. *Pinus* species generally show the isohydric characteristics (Klein *et al.*, 2011; Roman *et al.*, 2015). They constantly regulate the water loss within certain range to reduce the leaf water potential variability (Buckley, 2005). In isohydric species, G_{cref} and m show the conservative relationship, regardless of difference in species and climatic conditions (Oren *et al.*, 2001; Ewers *et al.*, 2005), which shown in this study also. In addition, leaf water potential is regulated within relatively constant ranges regardless of soil water status. This causes that similar relations between D and G_c can be found under various climatic conditions.

However, interannual differences in parameter value are also found (Fig. 4.5(c)). δ shows relatively larger interannual variations than other parameters, and this interannual variations has relations with annual mean θ (Fig. 4.6). The θ variation does not explain the inter plot differences in δ , but the mean δ is highest when annual mean θ is high, and is lowest when annual mean θ is lowest.

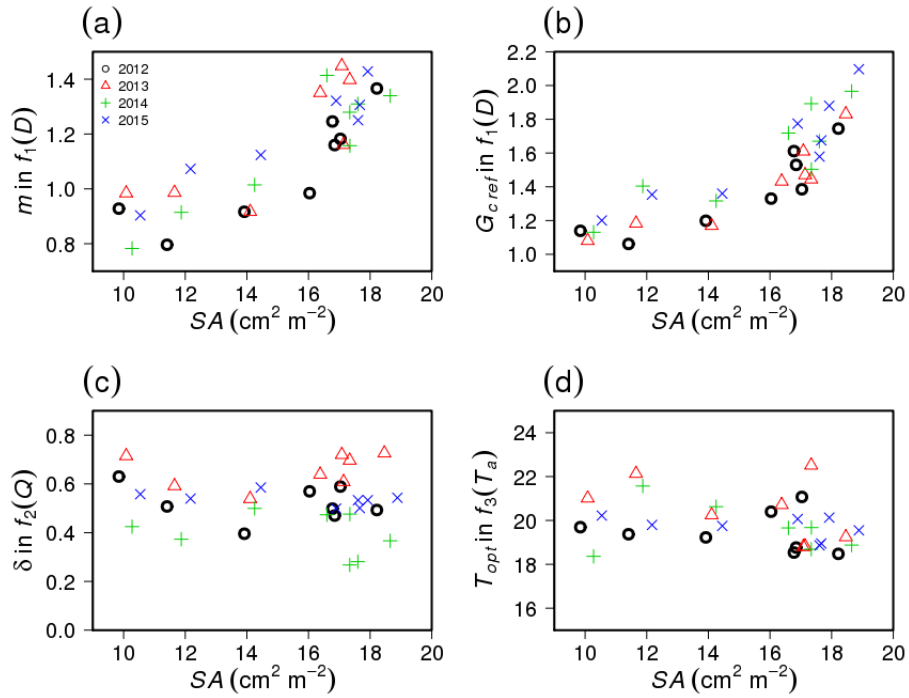


Figure 4.5. Interannual variation in relationship (a) between stand sapwood area (SA) and the slope (m) in $f_1(D)$, (b) between SA and the reference canopy conductance ($G_{c,ref}$) in $f_1(D)$, (c) between SA and regression coefficient (δ) in $f_2(Q)$, and (d) between SA and optimum air temperature (T_{opt}) in $f_3(T_a)$.

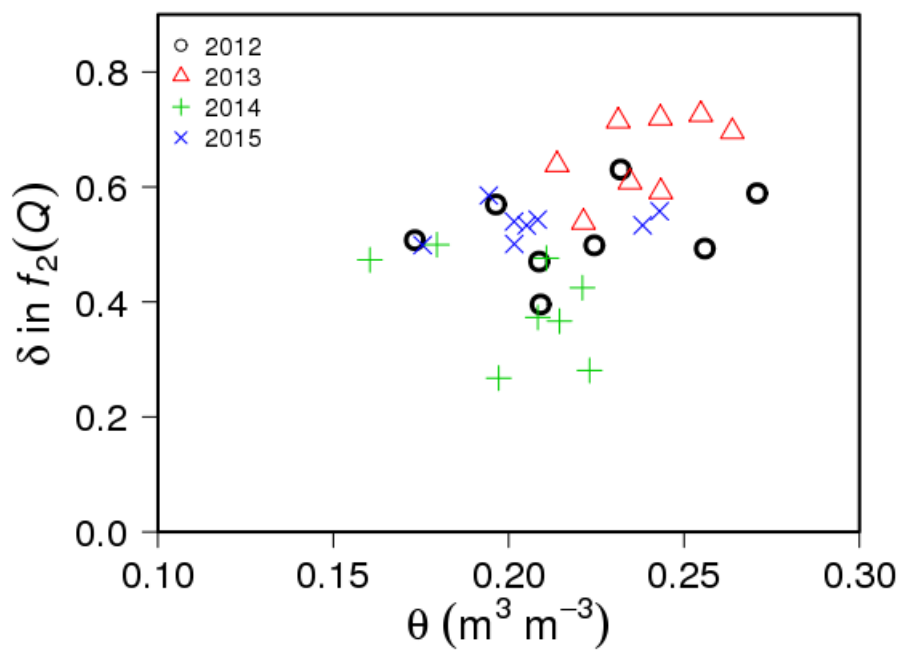


Figure 4.6. The comparison of interannual variation in soil water contents (θ) and δ

4.5.3 Limitations

Empirical approaches show high performance in limited ranges of environmental conditions. Since they have been developed under constrained ranges of environmental conditions, extreme climatic conditions like drought reduce the ability of them in estimation of G_c (Gao *et al.*, 2002). Thus, compatibility of empirical models depends on the generality of observed relationship, and the range where observed relationship is valid.

There are sources of uncertainty in upscaling from sapflux density measurements to stand transpiration. Even though measured radial and circumferential variation in sapflux density (Moon *et al.*, 2015) were used for upscaling, the assumption of similar radial variation regardless of stand sapwood area would not be valid, because the radial variation can be significantly changed by stand density (Medhurst *et al.*, 2002). In addition, the relationship in SA and LAI can be changed by stand density. In the less competitive plots, trees can access more water and nutrients, and allocate more biomass to aboveground. Trees in low stand density stand support more leaf area per unit basal area (Shibuya *et al.*, 2005).

In the simplification of Penman-Monteith equation, aerodynamic conductance is assumed as infinite. This assumption is generally accepted in forests (Herbst, 1995), but forest stand structure and surface roughness affect aerodynamic conductance. As results, applying simplified Penman-Monteith equation on stand with low aerodynamic conductance causes overestimation of canopy conductance.

4.5.4 Implications to forest management

The E_T model developed in this study would be very useful to estimated changes of E_T in Korean pine forests with forest management induced structural changes. Similar methods have been applied to predict E_T at various sites (Granier *et al.*, 2000b; Komatsu *et al.*, 2010), they are either too general to apply specific sites or too specific to find the spatial heterogeneity.

The E_T model also helps to estimate the spatial variation of E_T and total amount of forest water use with combined use of forest digital map and National Forest Inventory data. The most powerful aspect of this model is the use of simple and easily-measurable forest structural variable (SA). However, currently this model application is constrained to *Pinus koraiensis* forest. Direct application of empirical relationship found on this study to other type of forest could generate erroneous estimation of E_T , but the concept of this study would be useful to develop E_T model for forest composed with other species.

In addition, the model helps to estimate forest productivity also, because G_c can be regarded as proxy of gross primary productivity (Giorio *et al.*, 1999; Turnbull *et al.*, 2002).

4.6 Summary

This study develops stand transpiration model which relate stand structural variable with canopy conductance. Reference canopy conductance and stomatal sensitivity to vapor pressure deficit shows significant correlation with stand sapwood area. The model successfully reproduces the changes of stand transpiration against changes of stand sapwood area and climatic conditions.

The results indicate that measurement on single growing season on stand with various sapwood area could generate reliable stand

transpiration model for mono species forest. In addition, the use of simple forest structural variable could lead generality of this method, and enable the easy application to other forests. This would help to understanding the mechanisms underlying in the spatial and temporal variation of forest water use.

Chapter 5. Conclusion

The overall purpose of this study is to find causal relationships between thinning and physiological function and growth of trees in a Korean pine plantation. Especially, this study focused (1) on the effects of different thinning intensity on tree water use, productivity and water use efficiency, and (2) on the spatial and temporal variations of stand transpiration by heterogeneous stand sapwood area and climatic conditions.

In first step, this study shows that thinning enhanced the sap flux density and diameter growth. These positive effects of thinning on tree level water use and growth were more apparent in heavy-thinning treatment than light-thinning treatment. The interannual variations in water use efficiency indicated that light conditions might be the main driver of positive thinning effects. These results indicate that thinning by 40% removal of total trees is an appropriate management practice in mature pine forests compared to thinning by 20% removal, and this results in improved tree growth together without loss in water use efficiency.

Secondly, this study develops a stand transpiration model which relates stand structural variable with canopy conductance. Reference canopy conductance and stomatal sensitivity to vapor pressure deficit shows significant correlation with stand sapwood area. The model

successfully reproduces the changes of stand transpiration against changes of stand sapwood area and climatic conditions. These results indicate that measurement on single growing season on stand with various sapwood area could generate reliable stand transpiration model for mono species forest. In addition, the use of simple forest structural variable could lead generality of this method, and enable the easy application to other forests. This would help to understanding the mechanisms underlying in the spatial and temporal variation of forest water use.

In summary, this study helps to improve the understandings on the structure-function interactions in a 50-year-old Korean pine plantation by quantifying the changes of sap flux density, tree growth and water use, and water use efficiency by common forest management practices, thinning, and relating the forest stand structural variable (sapwood area) with stand transpiration.

However, there are several limitations in generalizing above findings for estimation of forest management effects. At first, this study covers for 4-year-long measurements periods. Up to my knowledge, this is the first study that both of tree water use and productivity are continuously measured with high temporal scales for four years in Korea, but four years might be a short period regarding to forest management planning. In addition, it is questionable that significant effects of heavy thinning treatment found in this study can be sustaining for long period. Secondly, thinning practice applied in this study might be different from

conventional selective thinning, which generally removes large trees in mature forests. Finally, the stand transpiration model developed in this study should be tested in other Korean pine forests. Therefore, further monitoring in same study site and other Korean pine forests is required.

Korean pine plantations have been intensively managed due to its high economic value, but the understanding of the effects of forest management practices has been limited. All of above results indicate the dependency of forest ecosystem function (productivity, water use, and water use efficiency) on forest ecosystem structure (stand density and sapwood area). Under careful consideration of limitations in this study, using these structure-function relationships enables to relate the forest management induced structural changes and changes of forest ecosystem function, and helps to make proper management planning for Korean pine plantations.

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초 록

산림 관리 효과의 기저 메커니즘을 이해하는 것은 산림 관리 계획에 있어 필수적이다. 주요 산림 관리 방법인 간벌은 산림의 미기상적 조건을 변화시키고, 이로 인해 생산성 및 증산과 같은 산림 기능이 변화하게 된다. 이러한 산림 관리 효과에 대한 연구가 많이 진행되고 있으며, 산림 관리 효과를 조절하는 기작에 대한 이해 역시 증가하고 있다. 하지만 연구 대상지의 조건이나 대상 주종에 따라 다양한 결과들이 보고되고 있다.

잣나무는 우리나라 주요 조림 수종 중 하나로, 목재와 열매 생산 등의 다양한 생태적 서비스를 제공하고 있다. 우리나라에 남아 있는 잣나무림은 대부분 조림에 의해 조성되었으며, 조림 이후 지속적인 산림 관리가 이루어지고 있다. 하지만 잣나무 조림지에서의 산림 관리가 미치는 영향에 대한 연구는 아직 부족한 상황이다. 따라서 이 연구는 다음의 두가지 목적을 갖고 진행하였다. 첫번째 목적은 V영급 잣나무 조림지에서 간벌 강도가 나무 수준의 물 이용, 생산성과 물이용효율에 미치는 영향을 정량화하는 것이다. 두번째 목적은 산림의 구조적 특성 중 하나인 임분 변재 면적과 임관전도도를 연결시켜, 임분 구조의 차이에 따른 임분 증산량의 변화를 예측할 수 있는 임분 증산 모델을 개발하는 것이다.

첫 번째 목적을 위해, V영급 잣나무림을 대상으로 두 가지 강도의 간벌을 시행하였으며, 간벌 이후 4년 동안 지속적으로 수분 이용량과 생산성을 모니터링하였다. 강도 간벌로 인해 개체 수준의

수분 이용량과 생산성이 유의하게 향상되었으나, 약도 간벌에서는 그 효과가 분명하지 않았다. 또한 나무 크기-생장 관계가 간벌 강도에 의해 달라짐을 확인할 수 있었다.

두 번째 목적을 위해, 서로 다른 구조적 특성을 보이는 임분에서 측정한 수액속밀도를 이용해 임관 전도도 모델을 개발하였다. 이 임관 전도도 모델은 포차, 광합성유효광, 기온, 토양 수분에 의한 단계적인 임관 전도도 제한을 모의한다. 기준 전도도와 포차에 대한 임관 전도도 민감도는 임분 변재 면적과 높은 상관관계를 보였다. 이러한 임관 전도도-변재 면적 관계를 고려하는 임분 증산량 모델은 임분 변재 면적의 변화와 환경 조건의 변화에 따른 임분 증산량 변화를 성공적으로 모의하였다.

이 연구에서 밝힌 간벌 강도에 따른 산림 기능의 변화와 임분 변재 면적의 변화에 따른 임분 증산량의 변화 경향은 잣나무림에서 산림 관리로 인한 산림 구조의 변화에 동반된 산림 기능 변화를 예측하는 데 도움을 주며, 산림 관리 계획에 있어 필수적인 정보를 제공할 수 있을 것이다.

주요어: 간벌, 변재 면적, 크기-생장 관계, 생산성, 증산량
학 번: 2011-31027